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NUMBER 36

BIOSYSTEMATICS OF THE GENUS *DICROTENDIPES* KIEFFER, 1913 (DIPTERA: CHIRONOMIDAE: CHIRONOMINAE) OF THE WORLD

By

John H. Epler

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Selwyn S. Roback
Editor

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TABLE OF CONTENTS

ABSTRACT 1
CHAPTER I. INTRODUCTION AND NOTES ON THE HOLARCTIC *DICROTENDIPES* 2
Methodology 3
Terminology and Morphology 4
Biology 4
Taxonomy 6
Notes on the Holarctic *Dicrotendipes* 12
Key to Adult Males of Holarctic *Dicrotendipes* 13
Key to Known Pupae of Holarctic *Dicrotendipes* 15
Key to Known 4th Instar Larvae of Holarctic *Dicrotendipes* 16
CHAPTER II. A REVIEW OF THE AFROTROPICAL *DICROTENDIPES,* WITH DESCRIPTIONS OF THE IMMATURE STAGES 32
Key to Adult Males of Afrotropical *Dicrotendipes* 33
CHAPTER III. THE NEOTROPICAL *DICROTENDIPES* 58
Key to Adult Males of Neotropical *Dicrotendipes* 58
CHAPTER IV. THE *DICROTENDIPES* OF THE ORIENTAL-AUSTRALASIAN REGION 110
Key to Adult Males of Oriental-Australasian *Dicrotendipes* 111
Key to Known Pupae of Oriental-Australasian *Dicrotendipes* 112
Key to Known Larvae of Oriental-Australasian *Dicrotendipes* 113
CHAPTER V. ZOOGEOGRAPHY 178
CHAPTER VI. PHYLOGENY 194
ACKNOWLEDGEMENTS 204
LITERATURE CITED 205
APPENDIX 1–List of recognized species names in the genus *Dicrotendipes,* and their distribution 211
APPENDIX 2–List of recent name changes and current name as recognized in this paper 212
INDEX 213

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BY

JOHN H. EPLER[1]

ABSTRACT — The taxonomy, zoogeography and phylogeny of the genus *Dicrotendipes* Kieffer, 1913 (Diptera: Chironomidae) are reviewed on a world-wide basis. Data from a previous study of the Nearctic fauna (Epler 1983, 1987a) are supplemented by studies of the Holarctic, Neotropical, Afrotropical, Oriental, Australian and Oceanian faunas. Seventy-two species names are recognized; the type-species of the genus is *Chironomus septemmaculatus* Becker, 1908.

Notes on the Holarctic fauna are provided; 25 species are recognized from the area. *Dicrotendipes incurvus* (Sublette, 1964) is considered a junior synonym of *D. tritomus* (Kieffer, 1916). Keys for the adult males, pupae and larvae of the *Dicrotendipes* of the Holarctic region are included.

The taxonomy of 14 species recognized from the Afrotropical region is reviewed; these are: *D. bredoi* (Goetghebuer, 1936), *D. chambiensis* (Goetghebuer, 1936), *D. collarti* (Goetghebuer, 1936), *D. cordatus* Kieffer, 1922, *D. ealae* (Freeman, 1957), *D. freemani* [nom. nov. for *D. binotatus* (Kieffer, 1911)], *D. fusconotatus* (Kieffer, 1922), *D. kribiicola* (Kieffer, 1923), *D. leucolabis* Kieffer, 1922, *D. nigrolineatus* (Freeman, 1957), *D. peringueyanus* Kieffer, 1924, *D. schoutedeni* (Goetghebuer, 1936), *D. septemmaculatus* (Becker, 1908) and *D. sudanicus* (Freeman, 1957). The larvae and pupae of *D. fusconotatus, D. kribiicola, D. septemmaculatus* and *D. sudanicus,* and the pupa of *D. cordatus* are described. New junior synonyms for *D. septemmaculatus* are: *D. formosanus* Kieffer, 1916, *D. frontalis* Kieffer, 1916, *Chironomus hirtitarsis* Johannsen, 1932, and *D. rajasthani* Singh & Kulshrestha, 1977; *Ch. punctatipennis* Kieffer, 1910 is considered a probable junior synonym. A key to adult males is provided.

Nineteen species are recorded from the Neotropical region. Previously described species discussed include: *D. aethiops* (Townes, 1945), *D. alsinensis* (Paggi, 1975), *D. californicus* (Johannsen, 1905), *D. crypticus* Epler, 1987, *D. embalsensis* Paggi, 1987, *D. nestori* Paggi, 1978, *D.*

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obrienorum Epler, 1987, *D. pellegriniensis* Paggi, 1987 and *D. sinoposus* Epler, 1987. The adult males of 10 new species are described: *D. amazonicus, D. dasylabidus, D. demissus, D. fittkaui, D. palearivillosus, D. paradasylabidus, D. paterjohni, D. radinovskyi, D. reissi* and *D. soccus;* adult females are described for *D. amazonicus* and *D. demissus;* and pupae are described for *D. fittkaui* and *D. reissi.* A key is provided to identify Neotropical adult males.

A total of 19 species are recognized from the combined Oriental, Australian and Oceanian regions. Three species previously considered to be *Dicrotendipes* are removed: *Ch. blandellus* Kieffer, 1906, *D. paxillus* Guha, Chaudhuri & Nandi, 1982, and *D. socionotus* Guha, Chaudhuri & Nandi, 1982. New species and stages described are: *D. balciunasi* (adult male), *D. cumberlandensis* (adult male and female, pupa, larva), *D. jobetus* (adult male), *D. jonmartini* (adult male, pupa, larva), *D. lindae* (adult male), *D. pseudoconjunctus* (adult male, pupa, larva) and *D. sarinae* (adult male and female, pupa, larva). The adult males and females are redescribed, and pupae and larvae described, for: *D. candidibasis* (Edwards, 1924), *D. conjunctus* (Walker, 1856) and *D. pelochloris* (Kieffer, 1912); adult males are redescribed for *D. bilobatus* Kieffer, 1917 and *D. tenuiforceps* (Kieffer, 1913). The pupa and larva of *D. flexus* (Johannsen, 1932) are redescribed, and the taxonomy of *D. leei* (Freeman, 1961) and *D. taylori* (Freeman, 1961) is reviewed; *D. semiviridis* is considered a *species inquirenda.* New synonyms include: *Ch. melanocnemis* Edwards, 1928 (junior synonym of *D. candidibasis); Limnochironomus niveicauda* Kieffer, 1921, *Ch. inferior* Johannsen, 1932, *Ch. (D.) wirthi* Freeman, 1961, *Xenochironomus loripes* Guha & Chaudhuri, 1981, *Kimius hoonsooi* Ree, 1981 (junior synonyms of *D. pelochloris*) and *Ch. (D.) innisfailensis* Freeman, 1961 (junior synonym of *D. tenuiforceps*); *D. bilobatus* is removed from synonymy with *D. conjunctus.* Keys are provided for adult males, pupae and larvae.

Distributions of selected species are discussed and distribution maps provided for *D. aethiops, D. californicus* complex, *D. flexus, D. lobiger, D. modestus, D. nervosus, D. pelochloris, D. septemmaculatus, D. sinoposus, D. tenuiforceps* and *D. tritomus.*

The phylogeny of *Dicrotendipes* species known in all 3 life stages is analyzed cladistically. Results indicate that 3 major lineages occur within the genus, with at least 9 species groups.

Chapter I.
Introduction and Notes on The Holarctic *Dicrotendipes*

The genus *Dicrotendipes* was recently revised for the Nearctic region (Epler 1987a). This monograph is basically a continuation of that revision, and includes general notes on the genus and the Holarctic species (Chapter I), a review of the Afrotropical species (Chapter II), a revision of the Neotropical species (Chapter III), and a revision of the species found in the combined Oriental, Australasian and Oceanian region (termed the Oriental-Australasian region in this paper) (Chapter IV). The zoogeography of selected species in the genus is discussed in Chapter V. A phylogenetic analysis is included in Chapter VI. Appendix 1 is a list of the recognized species (72) in the genus; Appendix 2 presents a list of the most recent synonymies in the genus.

Methodology

Methods used for specimen preparation and measurement are similar to those explained in Epler (1983, 1987a, 1987b). Most measurement methods are illustrated in Figs. 1–5. All measurements are in micrometers (μm) (unless stated otherwise) and consist of the range, mean, and, in parentheses, the number of specimens utilized if different from the number (n) cited at the beginning of the description.

All illustrations were drawn by the author. The hypopygial figures are drawn to show a ventral and internal view (of apodemes) on the left, and a dorsal view to the right. Lateral aspects of hypopygia are drawn with the gonocoxae and gonostyli removed. The dorsal hypopygial figures are drawn with the sensilla chaetica of the superior volsella as they may appear when viewed with a compound microscope, i.e., dorsal. In actuality the sensilla chaetica of the superior volsella are generally ventral (Fig. 3A).

Specimens examined in this study were borrowed from various individuals and/or institutions. The following abbreviations are used to denote collections from which material was borrowed or in which type material will be placed:

AN — Australian National Insect Collection, CSIRO, Canberra, Australia (D.H. Colless).
BM — British Museum (Natural History), London, England, U.K. (P.S. Cranston).
CU — Clemson University, Clemson, SC, U.S.A. (M.W. Heyn).
FS — Florida State Collection of Arthropods, Florida A & M University, Tallahassee, FL, U.S.A.
HH — H. Hashimoto, Shizuoka University, Shizuoka, Japan.
IL — Instituto de Limnologia, Universidad Nacional de la Plata, Berisso, Argentina (A.C. Paggi).
IN — Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
IP — Institut für Pflanzenschutzforschung Kleinmachnow, Eberswalde-Finow, D.D.R (H.J. Müller).
JB — J. Balciunas, Fort Lauderdale, FL, U.S.A.
JE — J.H. Epler, Florida A & M University, Tallahassee, FL, U.S.A.
JM — J. Martin, University of Melbourne, Melbourne, Australia.
KM — Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (E. DeConinck).
LH — L. Hare, Université du Quebec, Quebec, Canada.
NM — Naturhistorisches Museum, Vienna, Austria (R. Contreras-Lichtenberg).
SP — School of Public Health and Tropical Medicine, University of Sydney, Sydney, Australia (M.L. Debenham).

UB — University of Burdwan, Burdwan, India (P.K. Chaudhuri).
US — United States National Museum, Washington, D.C., U.S.A. (B.V. Peterson).
ZH — Zoologisches Museum, Humboldt University, Berlin, F.R.G (through P.S. Cranston).
ZM — Z.Moubayed, Université Paul Sabatier, Toulouse, France.
ZS — Zoologische Staatssammlung, Munich, F.R.G (E.J. Fittkau & F. Reiss).

Terminology and Morphology

Terminology and abbreviations for body parts and ratios follow Saether (1980) and Epler (1987a, 1987b), and are illustrated in Figs. 1–7. LWR refers to the length/width ratio of the superior volsella. See Epler (1987a) for a more detailed discussion of the morphology of *Dicrotendipes.* Some new terms are introduced here.

If setae present on the dorsum of the hypopygium (adult male) could not be distinguished as medial and/or dorsal basal setae, the combined term *dorsomedial setae* was used.

Freeman (1957:366) noted the presence of "5–6 black spines ventrally" on abdominal sternite VI of *D. cordatus* Kieffer. Epler (1987a) also noted the presence of "darker, flattened, bluntly tipped setae, which are easily lost" on most Nearctic species. Epler (1987b) referred to these setae as "flattened setae on S VI." Throughout the present monograph these setae, which are an apparent autapomorphy for *Dicrotendipes,* are termed *ventral accessory setae.* Although they are most often found on S VI, ventral accessory setae may also occur on S V and S VII, and are present on males and females of most species in the genus. They are absent from members of the *D. californicus* complex and the *septemmaculatus* group. Ventral accessory setae may appear as darker, more robust setae, as slightly flattened, darker and more robust setae, or as darker, stout spine-like setae (Fig. 1F).

I was mistaken in my Nearctic revision (Epler 1987a) when I stated that the large subquadrate to oval areas on the frontoclypeal apotome of *D. lobiger* (Kieffer) and the frontal apotome of *D. leucoscelis* (Townes) were dorsal (on the apotome). These areas are ventral (on the apotome) or internal. Similar areas are found on the larval frontal apotomes of *D. kribiicola* (Kieffer), *D. notatus* (Meigen), *D. conjunctus* (Walker) and its close relatives, and *D. pelochloris* (Kieffer).

Biology

Adults of *Dicrotendipes* have been considered as pests due to large emergences (Frommer & Rauch 1971; Ali & Mulla 1980), and have been implicated in allergic reactions in humans in Africa (Cranston et al. 1983).

The immature stages are found in both lentic and lotic habitats, but are generally more prevalent in lentic situations. The larvae in general are not "burrowers" as listed in Coffman & Ferrington (1984), but would be better classified as "clingers" and/or "sprawlers." Although often reported in the literature as "bottom-dwelling" (Roback 1957) or "epibenthic, unattached" (Beck 1977), the majority of *Dicrotendipes* larvae are found on the surface of aquatic vegetation, and among or on vegetation or Aufwuchs on rocks, logs, or similar substrata. The larvae construct silken tubes which are attached to the substrate. The pupal stage is also spent in the tube. I have rarely collected *Dicrotendipes* larvae from bottom mud, although larvae do occur commonly in algal mats on the bottom. Darby (1962) reported finding *D. californicus* (Johannsen) larvae on the surface of bottom mud in late May and early June in California, but found that as submerged vegetation increased, the vegetation became the favored habitat. Lenz (1954–1962) reported *Dicrotendipes* larvae (as *Limnochironomus*) as predominantly littoral and living on rocks, plant stems, and among aquatic vegetation, but also noted their existence in benthic detritus in water 10 m or more in depth, as well as among mosses and other vegetation on rocks in flowing water. I have found *D. fumidus* (Johannsen) on *Myriophyllum* and algae covered rocks, *D. lobus* (Beck) associated with *Najas, Juncus* and *Spartina* in salt marshes and *D. modestus* (Say) on *Myriophyllum* and *Typha;* and I have examined reared *D. candidibasis* (Edwards) specimens collected from streamside vegetation in Fiji and *D. septemmaculatus* larvae collected on *Hydrilla* from Burma, Indonesia and Malaysia. Edward (1964) found the larvae of *D. conjunctus* inhabiting "algal mats and slime." I have collected *D. crypticus* Epler larvae from vegetation on rocks in the swiftly flowing portions of a New Mexican creek; I have scraped *D. neomodestus* (Malloch) larvae from algae in sheets of water flowing over a dam in Pennsylvania, and have collected the apparent larva of *D. adnilus* Epler from periphyton from midstream rocks in the mountains of southeastern Arizona (Epler 1987a).

Hudson (1987:table 1) listed chironomid genera that have species with unusual larval habitats or life histories. Among the 9 unusual habitats were listed 2 in which *Dicrotendipes* larvae may be found. The first of these categories is "symbiotic." Disney (1975) found *D. peringueyanus* Kieffer living phoretically on the African river crabs *Potomonautes africanus* (A. Milne-Edwards) and *P. pobeguini* (Rathbun) in Cameroon. The second unusual larval habitat is "water held in plants." Epler (1987a) examined a *D. leucoscelis* larva which had been collected and reared from the water in a bromeliad from Florida. At least 4 species (*D. inouei* Hashimoto, *D. lobus* (Beck), *D. modestus* (Say) & *D. pallidicornis* (Goetghebuer)) occur in brackish water; 2 of which, *D. inouei* and *D. lobus,* apparently occur exclusively in brackish water. The larvae of *D. flexus* and *D. pelochloris* (as *inferior*) have been reported from hot springs (40°) from Sumatra (Lenz 1937).

Dicrotendipes larvae feed on algae, detritus, or the microorganisms associated with it. Lenz (1954–1962) reported that he observed larvae spinning small "catch-nets" within their tubes. By undulating their bodies, the larvae produced a current which forced water through the catch-net. After a period of time, the catch-net and its catch of detritus and microorganisms were consumed by the larvae. I have not observed feeding in *Dicrotendipes,* but many larval guts I've examined were packed with algae and detrital material. The larval undulations probably serve a respiratory function, introducing fresh water in the larval tube. I have also observed pupae undulating in their tubes.

Taxonomy

Kieffer (1913b:23) established the genus *Dicrotendipes* from African material, stating (my translation) "this genus differs from all others in that the inferior appendages of the male forceps are bifurcated." Only one species, *D. pictipennis,* was included, which by monotypy (International Code of Zoological Nomenclature (ICZN), Art. 68(d)) was the type-species for the genus. When Freeman (1957) relegated *Dicrotendipes* to subgeneric status within *Chironomus,* the epithet *pictipennis* became a junior secondary homonym of *Ch. pictipennis* Philippi, 1865. The next available name for this species was *quatuordecimpunctatum* Goetghebuer, originally described in *Polypedilum* by Goetghebuer (1936). Freeman (1957) considered *quatuordecimpunctatum* a subspecies of *D. pilosimanus* Kieffer, 1914; thus, *D. pilosimanus* became the type-species of *Dicrotendipes.* Although *Dicrotendipes* was later returned to full generic status (Hamilton et al. 1969), the name *D. pictipennis* was invalid under ICZN Art. 59(b), because it was a junior secondary homonym replaced before 1961. Cranston and Armitage (1988) rediscovered the holotype of *Chironomus septemmaculatus* Becker, 1908, and considered it to be a senior synonym of *D. pilosimanus* Kieffer, 1914. The correct name for the type-species of the genus is now *Ch. septemmaculatus* Becker.

The genus *Limnochironomus* was established from the Palaearctic by Kieffer (1920:166), who described the apex of the inferior volsella (appendage) as "sometimes simple, sometimes imperfectly bi- or trilobed." Several species were included. The type-species, by original designation, is *Tendipes falciformis* Kieffer, 1912. This species is a junior synonym of *Chironomus nervosus* Staeger, 1839.

Kieffer (1922) later described 3 more species in *Dicrotendipes: trilabis, cordatus,* and *leucolabis.* In his description of the inferior volsella of *D. cordatus,* Kieffer (1922:65) stated "the apex strongly broadened like a heart,

the 2 lobes not as long as wide, divided by a curved indentation." By including *cordatus* in *Dicrotendipes,* Kieffer expanded the concept of the genus. In the other species of *Dicrotendipes* he described, the apex of the inferior volsella is deeply bifid. However, the cordiform apex of the inferior volsella of *D. cordatus* would also fit the description of the same structure in *Limnochironomus,* as can be seen from Kieffer's figure (Kieffer 1922:fig. 66). My examination of the pupa of *D. cordatus* (see Chapter II) indicates that Kieffer was correct in including the species in *Dicrotendipes.*

Calochironomus was first mentioned by Kieffer (1921a) in a key to genera. No species were mentioned. In a later paper on African chironomids (Kieffer 1922:66), he included 6 species in the genus and designated the type-species as *fusconotatum,* which was described from a female.

Kieffer (1921b:590) established the genus *Carteria* based on material from the Philippines and Formosa, naming *Chironomus longilobus* (Kieffer, 1916) (originally described in *Tendipes*), as the type-species. However, *Carteria* was preoccupied by *Carteria* Diesing, 1866 (a protozoan), and was renamed *Carteronica* by Strand (1928).

Edwards' (1929) concept of *Chironomus* was much broader than that of the continental European workers (e.g. Thienemann) at that time. He did not consider *Limnochironomus* distinctive enough to rate subgeneric rank, but relegated it to his Group C of *Chironomus.*

Goetghebuer (1936, 1937–1954) also defined *Chironomus* in a broad sense. He considered *Carteria, Calochironomus, Dicrotendipes* and *Limnochironomus* to be subgenera of *Chironomus.* He apparently was unaware of Strand's 1928 paper renaming *Carteria* as *Carteronica.*

Aristovskaya (1935:114) established the genus *Sernowia* in a footnote, stating (loosely translated): "name at present for form previously described by N.N. Lipina as Chironominae genuinae No. 6." However, no type-species was designated. Pankratova's subsequent listing (in Chernovskii 1949) of Chironominae genuinae No. 6 and *Sernowia* (as *Sernovia*) as synonyms of *Limnochironomus* ex gr. *nervosus* Staeger does not satisfy the requirements for designation of a type-species (ICZN Art. 69). The name *Sernowia* thus becomes a *nomen nudum* and is not available (ICZN Art, 13(b)). *Sernowia* is also misspelled as "*Sernorwia*" in a table (Aristovskaya 1935:118).

Lenz (1937:6) described the larva and pupa of *Chironomus* (*Limnochironomus*) *flexus* Johannsen, 1932, and established it as a new genus, *Limnotendipes.* By monotypy, the type-species was *flexus.*

Cladotendipes was established by Lenz (1937) for a single species, *Chironomus inferior* Johannsen, 1932. Sublette and Sublette (1973) placed *Ch. inferior* in *Dicrotendipes,* but made no mention of *Cladotendipes.* See also Ashe (1983).

Townes (1945), in his comprehensive monograph of the Nearctic Chironomini (as Tendipedini), kept *Limnochironomus* as a subgenus of *Tendipes* (= *Chironomus*), and considered *Limnotendipes* a junior synonym.

Freeman (1955a) synonymized *Calochironomus* and *Limnochironomus* with *Dicrotendipes*. The type-species of *Calochironomus,* now known as *D. fusconotatus,* was described from a female. The male, apparently associated with the female by the pattern of wing spots and banded legs, has an inferior volsella with a deeply bifid apex, and is a *Dicrotendipes* in the sense of Kieffer's (1913b) original description of the genus. My examination of the immature stages (Chapter II) confirms this. Freeman also noted that the only species of *Calochironomus* in which the male was known to Kieffer, *C. oxylabis* Kieffer, 1922, was quite unlike the other species in the genus and was a *Chironomus* (*Einfeldia*). This species is now considered a junior synonym of *Chironomus formosipennis* Kieffer, 1908 (Freeman 1957; Freeman and Cranston 1980). Freeman (1955a) considered *Limnochironomus* a synonym of *Dicrotendipes* mainly because when Kieffer (1922) expanded the concept of *Dicrotendipes* by including *D. cordatus,* a species with a codiform apex to its inferior volsella, there was no longer a difference between the 2 genera. By Kieffer's (1920:106) own definition the inferior volsella of *Limnochironomus* could be imperfectly bi- or trilobed; a cordiform apex (as in *D. cordatus*) is imperfectly bilobed. As has been shown in Contreras-Lichtenberg (1986) and Epler (1987a), on the basis of the immature life stages *Limnochironomus* is a junior synonym of *Dicrotendipes*.

Freeman (1957) redefined *Chironomus* in much broader terms and included *Dicrotendipes* as a subgenus. He also synonymized *Carteria* and *Carteronica* with *Chironomus* (*Dicrotendipes*). The gonostylus of *Carteronica* species was very short and wide. Goetghebuer (1936:465) had described a species from Africa with a similar gonostylus, *Chironomus* (*Carteria*) *regalis,* and Freeman (1957) included this species and 2 new species with similar gonostyli, *penicillatus* and *multispinosus,* in his *Chironomus* (*Dicrotendipes*). He did not use structural similarities in the males to synonymize these 2 genera, but relied on similar thoracic color patterns of the females.

Hamilton et al. (1969) used the genus *Chironomus* in a stricter sense. Instead of a large genus with many subgenera, they preferred to use several smaller genera, in accordance with current European workers. *Dicrotendipes* was elevated back to the genus level.

Calochironomus and *Limnochironomus* are definitely junior synonyms of *Dicrotendipes*. However, *Carteronica* is not. This is based on examination of reared material of *Chironomus* (*Carteria*) *regalis* Goetghebuer and *Chironomus longilobus* (Kieffer) (type-species of *Carteronica*) from the Orient and Africa made available to me by Dr. L. Hare. *Carteronica* (replacement name for *Carteria* Kief-

fer, 1921) was removed from synonymy with *Dicrotendipes* (Epler 1987a). It should also be noted that the Afrotropical species which resemble *Carteronica* placed in *Dicrotendipes* by Freeman & Cranston (1980) (*crispi* Freeman, *multispinosus* Freeman, *penicillatus* Freeman and *regalis* Goetghebuer), are not *Carteronica,* but represent another, new, genus (manuscript in preparation).

Kimius, a monotypic genus established by Ree (1981) for the species *hoonsooi,* was included as a synonym of *D. niveicaudus* (Kieffer) (= *D. pelochloris*) by Sasa & Hasegawa (1983). I have seen specimens of this species and agree with the synonymy.

Generic synonyms are listed below. These are followed by an emended diagnosis for the genus incorporating new information discovered during the present study. A list of recognized species names (72) is given in Appendix 1. Appendix 2 is a list of recent specific synonymies in *Dicrotendipes.*

Genus *DICROTENDIPES* Kieffer

Dicrotendipes Kieffer 1913:23. Type-species: *Dicrotendipes pictipennis* Kieffer, 1913 (junior homonym, preoccupied by *pictipennis,* Philippi, 1865; = *Polypedilum quatuordecimpunctatum* Goetghebuer, 1936 = *Dicrotendipes pilosimanus* Kieffer, 1914 = *Chironomus septemmaculatus* Becker, 1908), by monotypy.

Limnochironomus Kieffer 1920:166. Type-species: *Tendipes falciformis* Kieffer, 1912, (= *nervosus* Staeger), by original designation.

nec *Carteria* Kieffer 1921b:590. Type-species: *Chironomus longilobus* (Kieffer, 1916), by original designation (junior homonym preoccupied by *Carteria* Diesing 1866); Freeman & Cranston 1980:190; Ashe 1983:15,21.

Calochironomus Kieffer 1921a:274. Type-species: *Calochironomus fusconotatum* Kieffer, 1922, by designation of Kieffer (1922:66).

nec *Carteronica* Strand 1928:48 (replacement name for *Carteria* Kieffer 1921); Freeman & Cranston 1980:190; Ashe 1983:15,21.

Chironomus (*Limnochironomus*), Goetghebuer 1928:50, Goetghebuer 1936:464, Goetghebuer 1937–1954:19.

Chironomus (*Chironomus*) Group C, Edwards 1929:386.

Sernowia Aristovskaya 1935:114. *Nomen nudum.* (No type-species designated).

nec *Chironomus* (*Carteria*), Goetghebuer 1936:465.

Chironomus (*Dicrotendipes*), Goetghebuer 1936:466; Goetghebuer 1937–1954:31.

Chironomus (*Calochironomus*), Goetghebuer 1936:467.

Chironomus (*sensu stricto*), Goetghebuer 1936:470 (partim).

Limnotendipes Lenz 1937:6. Type-species: *Chironomus* (*Limnochironomus*) *flexus* Johannsen, 1932, by monotypy.

Cladotendipes Lenz 1937:7. Type-species: *Chironomus inferior* Johannsen, 1932. by monotypy.

Tendipes (*Limnochronomus*), Townes 1945:102; Hauber & Morrissey 1945:287; Roback 1957:109.

Dicranotendipes Kruseman 1949:254 (misspelling).

Kimius Ree 1981:217. Type-species: *Kimius hoonsooi* Ree, 1981 (synonym of *D. pelochloris* (Kieffer, 1912)) by original designation; Sasa & Hasegawa 1983:321.

DESCRIPTION: **Adult male.** Medium sized chironomids, light yellow-green to dark green or light brown to dark red-brown. Legs sometimes banded, wings sometimes spotted or banded.

Eyes bare. Temporal setae in 1–3 rows beginning mesad to dorsomesal extension of eye, ending behind eye. Frontal tubercles present, small (2 μm) to medium (28 μm), very rarely absent. Antennal flagellum with 11 flagellomeres. Maxillary palp 5-segmented, basal segment weakly sclerotized and bearing one large lateral seta; segment 3 with specialized sensillae near apex. Clypeus subquadrate, setose. Cibarial setae present.

Antepronotum bare, narrowed and weakly notched dorsomesally. Thoracic scar well developed; humeral pit usually present dorsocaudally to thoracic scar. Scutal tubercle well to poorly developed, or absent. Acrostichal setae when present in double row (absent or reduced in some species), anteriorly beginning close to antepronotum and running posteriorly to anterior base of scutal tubercle (if present) or approximately mid-scutum. Dorsocentral setae in 1–3, usually 2, rows/side. Scutellar setae in 1–3 rows. Supraalar seta 1, rarely 2, /side. Prealar setae 2–7/side. Wing membrane without setae; squama with setal fringe. Brachiolum with 1–5 setae and 2 groups of campaniform sensilla; R, R_1 and R_{4+5} with setae; costa ends at R_{4+5}; FCu proximal, below, or distal to RM.

Metatarsal beard present or absent on foreleg, almost always present on hind leg. Foretibia with inner apical rounded scale which projects slightly beyond similar scale on outer tibial apex. Middle and hind tibiae with 2 combs each, barely separated, each comb bearing one spine which projects beyond others. Sensilla chaetica present on metatarsus of middle leg, usually confined to apical 1/5, occasionally running almost entire length of tarsomere; also sometimes present on hind metatarsus. Pulvilli 2 entire lobes; empodium thin, with sparse ventral fringe.

Abdominal sternite VI (and sometimes V or VII) with or without a medial group of ventral accessory setae, which are easily lost.

Gonostylus usually evenly curved on inner and outer margins, bearing one short, stout seta apically and several to many longer setae on inner preapical margin. Superior volsella well developed; digitiform, deltoid, pediform, elongate-cylindrical or bifid with sclerotized superior portion and membranous-lamelliform inferior portion; usually bare dorsally, bare or with microtrichia ventrally; often membranous apically; bearing several to many large sensilla chaetica on mesal and/or ventral surface. Inferior volsella well developed, usually strongly bowed dorsoventrally, usually with an expanded clubbed or slightly to deeply bifid or trifid apex bearing several to many long, strong sensilla chaetica. Rarely, a membranous median volsella present (2 species). Anal point of hypopygium pyriform to elongate-spatulate, occasionally with shelf-like basal lateral extension, usually slightly deflexed (strongly deflexed in some species).

Female. Generally similar to male; abdomen and wings stouter, and overall generally more setose than male. Genitalia with well developed dorsomesal and ventrolateral lobes; a well developed apodeme lobe present, usually covered with fine microtrichia (reduced in some species, very well developed in some species). Labia without microtrichia. Seminal capsules spherical to ovoid, with weak to moderate neck, spermathecal ducts without loops or bends.

Pupa. Light green to green or brown in life; exuviae almost colorless to dark brown. Cephalic tubercles present (essentially absent in *D. flexus*), poorly to well developed, broadly to narrowly conical, each with a short preapical frontal seta. Dorsum of thorax weakly to strongly granulose or pebbled, usually with a circular humeral callus lateroventral to base of thoracic horn. A scutal tubercle sometimes present. Thoracic horn with more than 50 branches emanating from 2 main trunks. Base of thoracic horn usually somewhat dumbbell-shaped, tracheal bundles usually separate (but joined in several species). Precorneal setae 2–3, dorsocentral setae 4, rarely 5.

Abdominal segment I without lateral setae, segments II–IV with 3 lateral hairlike setae, V–VII with 4 lateral lamellar setae, VIII with 4 or 5 lateral lamellar setae. Anal lobe with an anterior pair of dorsal setae, easily lost; a pair of dorsal caudolateral lamellar setae; and 30+

ventral lateral lamellar setae on each lobe, usually uniserial, at times partially biserial. An uninterrupted row of caudal hooklets on T II. Intersegmental conjunctiva of T III/IV-T V/VI usually with fine spinules. Sternites I–III with or without 1–2 transverse rows of spines. Caudolateral corners of VIII with one to many, weakly to strongly developed, straight to strongly sinuate spurs. Shagreen occasionally present on T I, present as fine longitudinal band(s) or generally spread spinules on S I. Ventral shagreen on S II and III present as 2–4 longitudinal bands connected by a transverse anterior band; weak to absent on S IV–VI (strongly developed in 1 species). Dorsal shagreen on T II–VI subquadrate, hourglass-shaped, or triangular in outline; often with small, separate elliptical to round anterolateral shagreen areas which may merge with median shagreen area. Segment VII often with rounded anterolateral shagreen areas, better developed dorsally. Dorsal shagreen of VIII usually U-shaped, or 2 longitudinal bands, or a pair of anterior and caudal oval to round areas, or almost completely covering dorsal area (*D. flexus*); ventral shagreen of VIII at most a weak copy of dorsal pattern, usually more reduced. Small caudolateral spine groups present on T V–VII. Pedes spurii A well developed on S IV. Pedes spurii B present on II. Segments II–VIII with one dorsal and one ventral pair O-setae. Segment I with 2–3 ventral, 2–4 dorsal pairs of setae; II with 3–4 ventral, 3–5 dorsal pairs; III with 3–4 ventral, 5 dorsal pairs; IV–VII with 4 ventral, 5 dorsal pairs; VIII with 1 ventral and 1 dorsal pair of setae. T VIII usually with small posterolateral dorsal lobes mediad of caudolateral spurs. In species with larvae possessing ventral tubules, weak ventral tubules should be present caudolaterally on S VIII (I have not yet observed such tubules on *Dicrotendipes* pupae).

Larva. Body pale green to green suffused with cream and/or red in life. Head capsule pale yellow to red-brown, often with a dark middorsal stripe over frontal apotome; postmentum often darker than remainder of head capsule. Mentum and mandibular teeth dark red-brown to black. Three pairs of eyespots, the ventral 2 pairs often joined, giving the appearance of only 2 pairs of eyespots. Dorsal eyespot largest, roughly oval to triangular in outline.

Antenna with 5 segments, segment 1 2–4X longer than second, segment 4 greater or approximately equal to 3. Antennal blade arises from apex of segment 1, reaching to 4th or 5th segment. Lauterborn organs and well developed style present at apex of segment 2.

Frontal apotome usually concave and roughly tuberculate along frontal suture, sometimes fused with 1st labral sclerite (forming a frontoclypeal apotome); usually with a small to large ventral anteromedian frontal pit and/or frontal process; or a larger ventral suboval to subquadrate area. Labrum with setae I–IVA + B present; S I moderately plumose; S II large, unfringed; S III hairlike; S IVA small, 2-segmented, S IVB subequal to S IVA, simple. Laterad to S II is a group of 3 fringed labral chaetae, subequal to S II, and 3–4 smaller chaetae. Labral lamella with fringe of 20–75 teeth. Pecten epipharyngis usually with 3–9, rarely 10–13, usually rounded, ventral lobes. 5–8 chaetulae laterales. Premandible distally bifid, the inner blade subequal to 2–3X wider than outer blade; 1–3 inner medial teeth usually present; a medial premandibular brush present.

Mandible with apical tooth, 1–2 dorsal preapical teeth, and 3 inner teeth, the proximal inner tooth sometimes modified. Pecten mandibularis composed of 6–18 strong setae. Seta subdentalis widest at middle, 4–7 times longer than wide; sometimes with accessory tooth. Seta interna with 4 main branches, united basally.

Mentum with 11–13 teeth, the median tooth and 1st laterals usually subequal, median tooth often notched mesolaterally, 2nd lateral tooth often fused or partially fused with 1st lateral; 5th and 6th lateral teeth sometimes rounded and fused. Ventromental plates 1.4X–2.2X wider than long, deeply striate, with smooth or crenulated anterior margin. Setae submenti usually simple, sometimes distally divided in many species.

Triangulum occipitale very narrow, scarcely visible in ventral view.

Ventral tubules usually absent, occasionally 1 pair present on 8th abdominal segment. Procercus wider than long or as wide as long, with 6–8 apical setae; 2 anterolateral preapical setae located on lightly sclerotized preapical plate. A pair of well developed supraanal setae present. Two pairs of anal tubules, usually somewhat conical, sometimes rounded and reduced (in brackish water species); ventral pair usually larger than dorsal pair.

Notes on the Holarctic *Dicrotendipes*

Epler (1987a) revised the Nearctic *Dicrotendipes*. The western Palaearctic species have recently been revised (Contreras-Lichtenberg 1986). A considerable amount of Palaearctic material, mostly of species with western Holarctic distributions, was available and is included in this study. In addition, eastern Palaearctic material of *D. pelochloris* (see Chap. IV) and *D. septemmaculatus* (see Chap. II) was available. Two additional species have recently been described from the eastern Palaearctic: *D. inouei* Hashimoto, 1984 and *D. tamaviridis* Sasa, 1981. Because the descriptions of these species are incomplete and no material was made available to me, *D. inouei* and *D. tamaviridis* are not included in this study.

Epler (1987a:51) noted the similarities between the immature stages of *D. incurvus* (Sublette, 1964) and *D. tritomus* (Kieffer, 1916), but had insufficient comparative material to make a more definite statement. Observing the illustration of *D. tritomus* (as *Limnochironomus*) in Pinder (1978:Fig. 158B), I erroneously stated that the apex of the superior volsella of *D tritomus* was turned out, not in as in *D. incurvus*. Recent examination of additional reared Palaearctic material of *D. tritomus* (through the kindness of Drs. P.H. Langton and F. Reiss) and Contreras-Lichtenberg's (1986:Fig. 14) recent redescription and illustration of this species revealed that the apex of the superior volsella of *D. tritomus* is directed mesad. The adult was originally described (Thienemann & Kieffer 1916) as having a trifid apex on the inferior volsella, or at least 3 apicodorsal rows of sensilla chaetica (Contreras-Lichtenberg 1986). Contreras-Lichtenberg (1986:671) used the number of dorsal rows of sensilla chaetica and the bifid or trifid nature of the apex of the inferior volsella as a secondary character in her key to separate *D. tritomus* from *D. modestus* (Say). However, many specimens, particularly from the Nearctic (*D. incurvus*), possess only a bifid apex, or 2 rows of apicodorsal sensilla chaetica (although I have also seen many Nearctic specimens with 3 dorsal rows), and Goetghebuer (1937–1954:19) stated in his key that the apex could be bifid or trifid. I have examined many specimens of *D. modestus* which have 3 or more rows of apicodorsal sensilla chaetica on the inferior volsella (see Epler 1987a:71; Fig. 92).

The immature stages of *D. incurvus* and *D. tritomus* are also inseparable to me and I conclude that the 2 species are synonymous. The holotype of

D. tritomus, as many of Kieffer's species, is apparently lost; I have not located one and Contreras-Lichtenberg did not examine it. I am using *D. tritomus* here in the sense of Lenz (1954–1962), Langton (1984), Pinder (1978) and Contreras-Lichtenberg (1986). Thus, *D. tritomus* is the fourth species of *Dicrotendipes* with a Holarctic distribution (see Chap. V).

The character, the presence of a second dorsal mandibular tooth, that Contreras-Lichtenberg (1986:670) uses for separating the larvae of *D. modestus* and *D. tritomus* is not reliable. I have seen a specimen of *D. tritomus* from Great Britain without a second tooth, and have seen many specimens of *D. modestus* with a second dorsal tooth or at least a definite large notch in the dorsal tooth. The second dorsal tooth is often difficult to observe unless the mandible is positioned correctly. The larvae of these 2 species are difficult to separate; usually the count of the ventromental plate strial ridges and differences in postmental coloration will separate them (see key below), but specimens must be reared to confirm species identity. Likewise, Contreras-Lichtenberg's (1986) pupal key will fail to separate these 2 species.

The pupa of *D. peringueyanus* as described by Contreras-Lichtenberg (1986) is not separable from *D. fusconotatus* or *D. pallidicornis* (see also Chap. II). In her pupal key, Contreras-Lichtenberg (1986) separates *D. peringueyanus* from *D. pallidicornis* based on the absence of conjunctival spinules on *D. pallidicornis.* However, all specimens of *D. pallidicornis* which I have examined do possess these spinules.

The following keys are offered for the identification of all known life stages (excepting the adult females) of the Holarctic *Dicrotendipes.* The reader is advised to consult the illustrations, descriptions and diagnoses in Contreras-Lichtenberg (1986) and Epler (1987a).

Key to Adult Males of Holarctic *Dicrotendipes*

(*D. inouei, D. tamaviridis* not included)

1. Inferior volsella deeply bifid apically; Palaearctic species 2
   Inferior volsella with simple apex, at most notched, appearing shallowly bifid or trifid; Holarctic species 5
2. Wings with spots or bands, or clouds along veins 3
   Wings immaculate. . . . . *D. pallidicornis* (Goetghebuer)
3. Small, membranous, triangular flap-like appendages present near base of anal point . . . . . *D. fusconotatus* (Kieffer)
   Base of anal point without appendages. 4
4. Wing with 6–7 well-defined spots, with 1 spot usually present in cell m_{3+4} . . . . . *D. septemmaculatus* (Becker)
   Wing with weakly defined spots, none present in cell m_{3+4} . *D. peringueyanus* Kieffer
5. Inferior volsella with membranous dorsal extension; Palaearctic . *D. notatus* (Meigen)
   Inferior volsella without membranous dorsal extension; Holarctic 6

6. Anal point sharply reflexed ventrad, usually not visible in dorsal view (Fig. 36); eastern Palaearctic . . . . . *D. pelochloris* (Kieffer)
   Anal point not sharply reflexed ventrad, visible in dorsal view; Holarctic 7
7. Superior volsella strongly pediform, apex directed outward; or triangular 8
   Superior volsella digitiform, long and slender, or long with weakly expanded membranous apex; if somewhat pediform, then apex directed inward 14
8. Superior volsella triangular, or if weakly pediform, sensilla chaetica restricted to posterior margin of superior volsella; coastal, brackish water species of SE U.S.A. . . . . *D. lobus* (Beck)
   Superior volsella pediform; sensilla chaetica not restricted to posterior margin of volsella 9
9. Legs strongly banded; Nearactic species . . . . . *D. californicus* complex 10
   Legs not banded, at most distal portions of some leg segments darker; Holarctic species 11
10. AR 2.13–2.36, mean 2.29; SV_2 4.15–4.41, mean 4.29; SV_3 2.71–2.89, mean 2.80; known from central and eastern New Mexico and Imperial Dam vicinity, California (possibly Kansas) . . . . . *D. crypticus* Epler
    AR 2.29–2.69, mean 2.47, SV_2 3.81–4.42, mean 4.07; SV_3 2.61–2.84, mean 2.71; widespread in western U.S. and Mexico . . . . . *D. californicus* (Johannsen)
11. Anal point with raised truncate base; known only from Chiricahua Mountains of SE Arizona . . . . . *D. adnilus* Epler
    Anal point not as above; widespread 12
12. Dorsum of tergite IX with many long setae laterad of anal point; SE U.S.A. . . . . *D. thanatogratus* Epler
    Dorsum of tergite IX not as above 13
13. Gonostylus inflated medially, narrowed proximally and preapically; general coloration brown; Nearctic . . . . . *D. neomodestus* (Malloch)
    Gonostylus not as above; general coloration green to red-brown; Holarctic . . . . . *D. modestus* (Say)
14. Superior volsella short, digitiform 15
    Superior volsella long and slender or long with weakly expanded membranous apex 18
15. Anal point with wide shelf-like base, tapering gradually to apex; superior volsella cylindrical, with slightly out-turned apex; Nearctic . . . . . *D. fumidus* (Johannsen)
    Anal point spatulate or narrowed at base 16
16. Superior volsella with thin membranous preapical extension; metatarsi usually with wide basal white band (lacking in most Florida specimens); Nearctic . . . . . *D. leucoscelis* (Townes)
    Superior volsella not as above; metatarsi without wide basal white band 17
17. Anal point long, narrowly spatulate; superior volsella with sclerotized area at apex; Holarctic . . . . . *D. lobiger* (Kieffer)
    Anal point and superior volsella not as above 18
18. Superior volsella long, slender, recurved, with an acute apex . . *D. botaurus* (Townes)
    Superior volsella not as above 19
19. Apex of superior volsella turned in 20
    Apex of superior volsella turned out; or straight, semiglobose 21
20. Gonostylus long, thin, and strongly curved; superior volsella usually without microtrichia; apex at most semimembranous; Nearctic . . . . . *D. milleri* (Townes)
    Gonostylus not as above; at least basal half of superior volsella with microtrichia, apex membranous; Holarctic . . . . . *D. tritomus* (Kieffer)

21. Superior volsella cylindrical, curving outward; apex bare, not expanded (Fig. 13); thorax with well developed scutal tubercle; SW U.S.A., Mexico . . *D. aethiops* (Townes)
Superior volsella not as above, apex expanded or inflated; thorax with or without scutal tubercle, widespread 22
22. Sensilla chaetica of superior volsella in a line often reaching middle of appendage tip, not directed exclusively inward; length of superior volsella 2–3.25X maximum width; wing with more than 35 setae on R & R_1; Holarctic . . . . . *D. nervosus* (Staeger)
Sensilla chaetica of superior volsella distributed on inner surface of appendage, the majority directed inward; length of superior volsella 4.25–5.25X maximum width; wing with 35 or fewer setae on R & R_1; Nearctic . . . . . *D. lucifer* complex (*D. lucifer* (Johannsen), *D. simpsoni* Epler). (*D. inouei* Hashimoto & *D. tamaviridis* Sasa, both eastern Palaearctic species, may key out here.)

Key to Known Pupae of Holarctic *Dicrotendipes*

1. Ventral spine row(s) present on S II 8
Ventral spine row(s) absent 2
2. 4 lateral lamellar setae on T VIII 3
5 lateral lamellar setae on T VIII 5
3. Shagreen spinules on T II–V largest posteriorly, tips often rounded; exuviae light yellow-brown to dark yellow-brown; Nearctic . . . . . *D. fumidus*
Shagreen spinules on T II–V more or less equal; exuviae clear or light to dark brown; Holarctic 4
4. Median shagreen spinules more or less equal on T VI; exuviae light to dark brown; strongly reticulate cuticular pattern on T VI–VIII, especially on T VI; coastal, brackish water species of SE U.S.A. . . . . *D. lobus*
Median shagreen area on T VI with longest spinules in middle of area; exuviae clear with yellowish borders; reticulate cuticular pattern on T VI–VIII at most moderately developed; Holarctic . . . . . *D. nervosus* group (*D. lucifer, D. nervosus, D. simpsoni*). (*D. tamaviridis* may key here.)
5. Anal lobe with dorsal shagreen; Palaearctic . . . . . *D. septemmaculatus* group (*D. fusconotatus, D. pallidicornis, D. peringueyanus, D. septemmaculatus*)
Anal lobe without dorsal shagreen 6
6. Intersegmental spines present between T V and T VI; Nearctic and western Palaearctic species 7
T V and T VI without intersegmental spines (Fig. 41J); eastern Palaearctic . . . . . *D. pelochloris*
7. Nearctic species . . . . . *D. leucoscelis*
Palaearctic species . . . . . *D. notatus*
8. 5 lateral setae on T VIII . . . . . *D. lobiger*
4 lateral setae on T VIII 9
9. Caudolateral spur on T VIII double or triple, spurs well separated 10
Caudolateral spur on T VIII single or closely appressed double 11
10. Cephalic tubercles long, thin, sharply acute, 33–40, mean 37, anal fin setae; New York, Indiana, Michigan, Minnesota, Oregon, Ontario and Manitoba . . . . . *D. milleri*
Cephalic tubercles shorter, wider; 33–55, mean 45, anal fin setae; Holarctic . . . . . *D. tritomus*

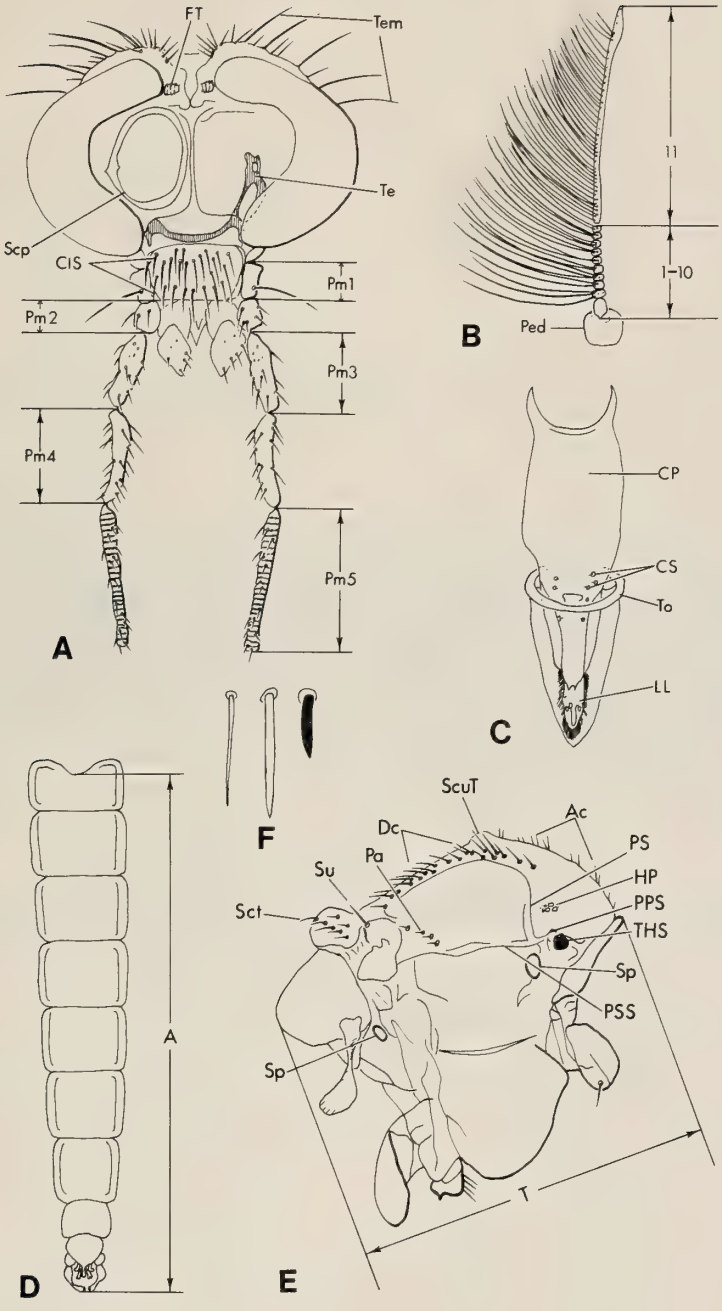
11. Median shagreen area on T VI with larger anterior and/or posterior spinules; widespread 12
Median shagreen spinules on T VI largest anteriorly only or those of posterior portion only slightly larger than middle; west and southwest U.S.A. . . . . .*D. californicus* complex (*D. californicus, D. crypticus*)
12. Dorsum of anal disc with thinly spined anteromesal shagreen areas; known only from Florida . . . . . .*D. thanatogratus*
Dorsum of anal disc without shagreen 13
13. Anterior and posterior spinules of median shagreen area on T VI more strongly developed than those of center; caudolateral spur on T VIII usually strongly recurved or sinuate 14
Posterior spinules of median shagreen area on T VI larger, more rounded or longer than those of anterior portion of shagreen area; caudolateral spur on T VIII not strongly sinuate or recurved, almost straight . . . . . .*D. tritomus*
14. Anal lobe with 31–50, mean 38, lateral setae; Nearctic. . . . . *D. neomodestus*
Anal lobe with 30–64, mean 50, lateral setae (1 specimen seen from Florida with only 30–33 anal lobe setae); Holarctic . . . . . *D. modestus*

Key to Known 4th Instar Larvae of Holarctic *Dicrotendipes*

1. Frontal apotome with a large anteromesal oval or subquadrate area; frontal pit or process absent 2
Frontal apotome without such an area; a small anteromedian frontal pit or frontal process usually present 5
2. A frontoclypeal apotome present; sixth lateral tooth of mentum well developed; 30–41, mean 35, ventromental strial ridges . . . . . .*D. lobiger*
A frontal apotome present; sixth lateral tooth of mentum reduced or closely appressed to 5th 3
3. Palaearctic species 4
Nearctic species; 37–60, mean 52 ventromental strial ridges . . . . . .*D. leucoscelis*
4. Eastern Palaearctic species; 30–34, mean 32 ventromental strial ridges (Fig. 41N) . . . . . *D. pelochloris*
Western Palaearctic species; about 40 ventromental strial ridges . . . . . *D. notatus*
5. Second lateral tooth of mentum almost completely fused with or closely appressed to 1st so that 1st lateral tooth appears notched (Fig. 13) 6
Second lateral tooth at most only partially fused to 1st lateral at base, 1st lateral tooth not appearing notched 9
6. Head capsule integument appears coarsely granular at 400X; Nearctic species . . . 16
Head capsule integument at most appears slightly granular at 400X; Nearctic or Palaearctic species 7
7. A long, ventral frontal process present on anteromedian margin of frontal apotome; Palaearctic only . . . . . .*D. septemmaculatus*
Long frontal process absent, but a frontal pit usually present; Nearctic only 8
8. Anal tubules reduced; anterior margin of ventromental plate mostly smooth; coastal, brackish water species of SE U.S.A. . . . . *D. lobus*
Anal tubules normal; at least anterior outer margin of ventromental plate usually crenulated; widespread in Nearctic . . . . . *D. neomodestus*
9. 60–70 ventromental strial ridges; Palaearctic only. . . . . *D. pallidicornis*
Less than 50 ventromental strial ridges; Nearctic or Palaearctic. 10

10. Ventromental plate with 22 or fewer strial ridges; anterior margin deeply scalloped 11
Ventromental plate with more than 22 strial ridges; anterior margin smooth or with shallow to moderate crenulations 12
11. Nearctic species (known only from Florida) . . . . . *D. thanatogratus*
Palaearctic species . . . . . *D. fusconotatus*
12. Proximal tooth of mandible saddle-shaped or with 2 points; or with inner surface of mandible adjacent to proximal tooth with deep semicircular incision; Nearctic. 13
Proximal tooth of mandible mostly triangular in outline, not as above; Holarctic . 14
13. Sixth lateral tooth of mentum rounded and closely appressed or fused to 5th lateral tooth; inner surface of mandible adjacent to proximal tooth with deep semicircular incision . . . . . *D. simpsoni*
Sixth lateral tooth of mentum pointed; inner surface of mandible adjacent to proximal tooth without deep semicircular incision . . . . . *D. lucifer*
14. Sixth lateral tooth of mentum rounded and closely appressed or fused to 5th lateral tooth . . . . . *D. nervosus*
Sixth lateral tooth pointed, separate 15
15. Head capsule integument appears coarsely granular at 400X; head capsule color yellow-brown to yellow-red-brown; Nearctic species 16
Head capsule integument at most appears slightly granular at 400X; head capsule color light brown to brown or pale yellow; Holarctic species 18
16. Postmentum or posterior portion of head capsule usually not darkened; 1st lateral teeth of mentum often turned outward; occurs throughout the Nearctic. . . *D. fumidus*
Postmentum or posterior portion of head capsule much darker than rest of head capsule; 1st lateral teeth of mentum rarely turned outward; western U.S.A. 17
17. Ventromental plate with crenulated anterior margin; 23–28, mean 25, ventromental strial ridges; known from central and eastern New Mexico and Imperial Dam vicinity, California (possibly Kansas) . . . . . *D. crypticus*
Ventromental plate with smooth anterior margin; 34–42, mean 37, ventromental strial ridges; widespread in western U.S.A. . . . . *D. californicus*
18. Head capsule pale yellow 19
Head capsule light brown to brown 20
19. Ventromental strial ridges 28–36, mean 32; postmentum usually darkened . . . . . *D. modestus*
Ventromental strial ridges 23–29, mean 25; postmentum rarely darkened . *D. tritomus*
20. Anterior margin of ventromental plates mostly smooth; known only from Chiricahua Mountains of SE Arizona . . . . . *D. adnilus*
Anterior margin of ventromental plates with shallow to moderate crenulations; widespread in Holarctic . . . . . *D. modestus*

FIG. 1. Adult morphology. A) Structures of head, frontal view. B) Antennal flagellum and pedicel; AR measurement method. C) Cibarial pump and associated structures. D) Method of abdominal length measurement. E) Thoracic structures. F) Ventral accessory setae of (left to right): *D. neomodestus, D. leucoscelis, D. cordatus.* (A, abdominal length; Ac, acrostichal setae; Cls, clypeal setae; CP, cibarial pump; CS, cibarial setae; Dc, dorsocentral setae; HP, humeral pit; LL, labial lonchus; Pa, prealar setae; Ped, pedicel; Pm_{1-5}, maxillary palpomeres 1-5; PPS, postpronotal suture; PS, parapsidal suture; PSS, prescutoscutal suture; Scp, scape; Sct, scutellar setae; Scut, scutellar tubercle; Sp, spiracle; Su, supraalar seta; T, thorax length; Te, tentorium; Tem, temporal setae; THS, thoracic scar; To, torma.)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ScuT
Ac
Dc
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Su
HP
PPS
Sct
THS
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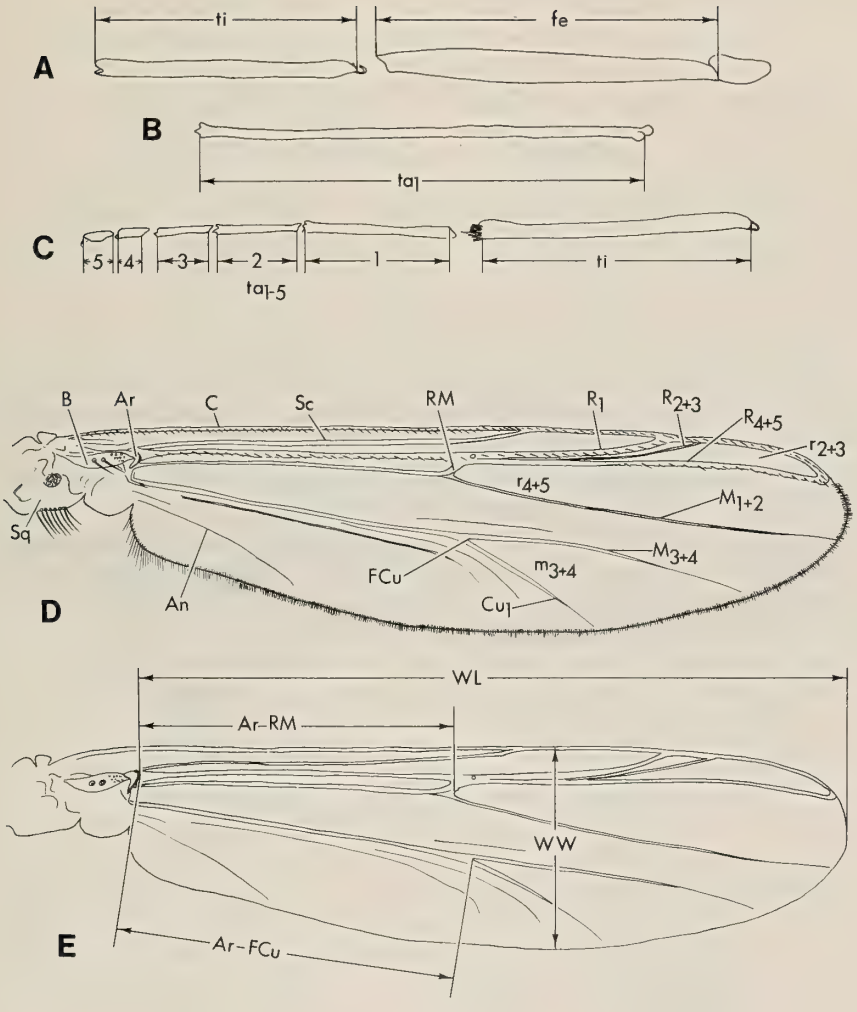
FIG. 2. Adult morphology. A) Method of measuring all femora & the fore tibia. B) Method of measuring fore metatarsus. C) Method of measuring tibiae & tarsomeres of mid & hind legs. D) Wing (see Saether 1980 for abbreviations). E) Methods of wing measurement. (WL, wing length; WW, wing width.)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1
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ta1-5
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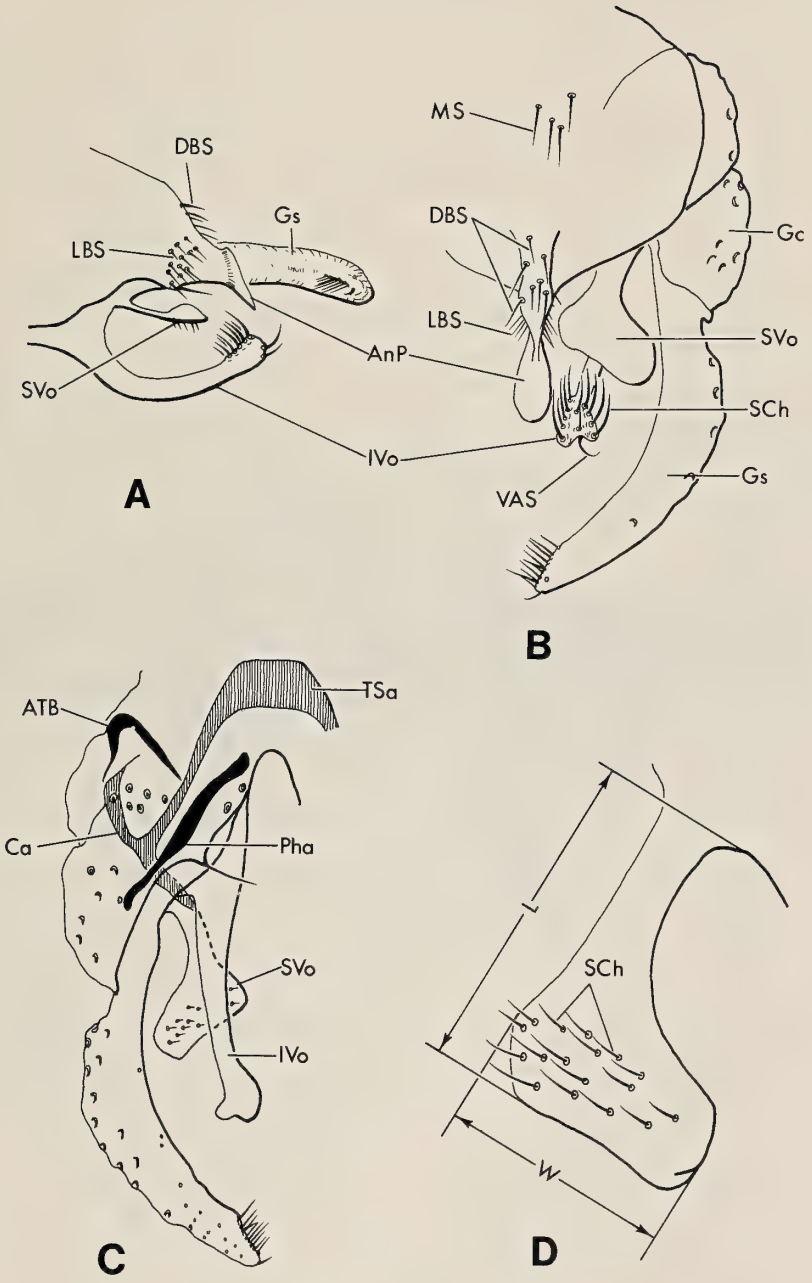
C
Sc
RM
R1
R2+3
R4+5
r2+3
r4+5
M1+2
M3+4
m3+4
Cu1
FCu
Sq
An
D
WL
Ar-RM
WW
Ar-FCu
E

FIG. 3. Adult male morphology. A) Lateral view of hypopygium (nearest gonostylus, inferior & superior volsellae removed). B) Dorsal view of right side of hypopygium. C) Ventral view of right side of hypopygium, showing internal apodemes. D) Ventral view, superior volsella. (AnP, anal point; ATB, anal tergal band; Ca, coxapodeme; DBS, dorsal basal setae; Gc, gonocoxite; Gs, gonostylus; IVo, inferior volsella; L, length of superior volsella; LBS, lateral basal setae; MS, median setae; Pha, phallapodeme; SCh, sensilla chaetica; SVo, superior volsella; TSa, transverse sternapodeme; VAS, ventral apical seta; W, width of superior volsella.)


DBS
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B
ATB
TSa
Ca
Pha
SVo
IVo
C
L
SCh
W
D

FIG. 4. Adult female morphology: A) Ventral view of terminalia. B) DmL and VlL. C) ApL. (ApL, apodeme lobe; Ce, cercus; Csa, coxosternapodeme; DmL, dorsomesal lobe; Gc IX, gonocoxite IX; SCa, seminal capsule; S VIII, sternite VIII; VlL, ventrolateral lobe; X, segment X.)

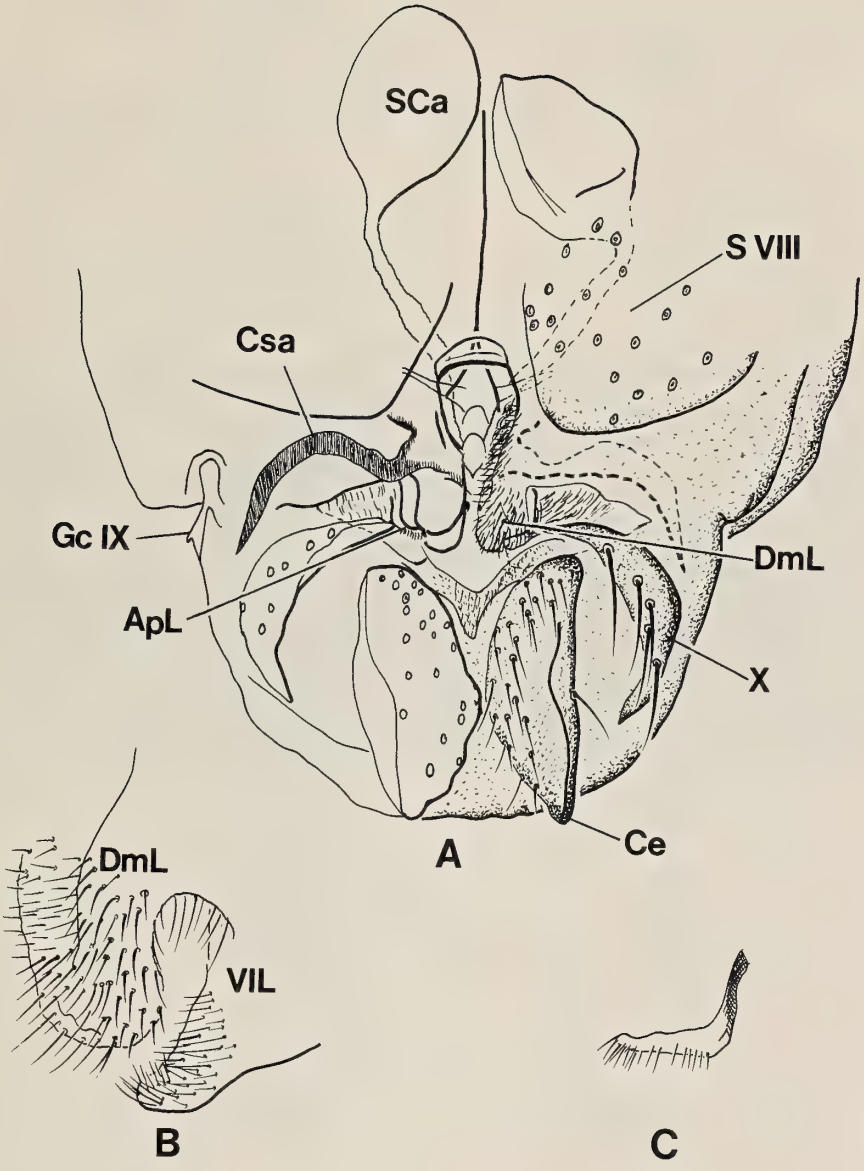
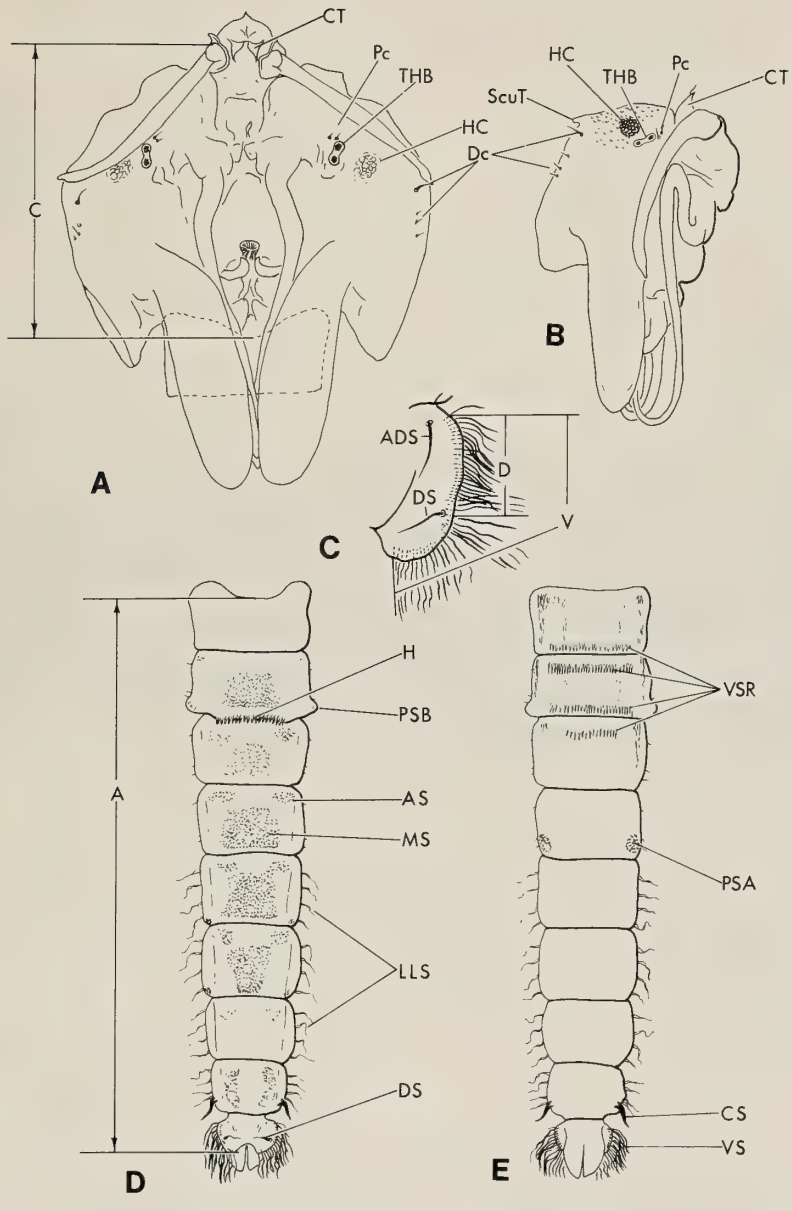

SCa
S VIII
Csa
Gc IX
DmL
ApL
X
Ce
A
DmL
VIL
B
C

FIG. 5. Pupal morphology. A) Ventral view of spread cephalothorax. B) Lateral view of cephalothorax. C) Dorsal view of anal lobe, depicting method of calculating disc ratio, DR. DR is the total number of ventral anal lobe setae (V) divided by the number of ventral setae anterior to and including dorsal seta position (D); DR = V/D. D) Dorsal view abdomen. E) Ventral view of abdomen. (A, abdomen length; ADS, anterodorsal seta; AS, anterolateral shagreen area; C, cephalothoracic length; CS, caudolateral spur; CT, cephalic tubercle; D, number of ventral setae from dorsal seta position to anterior margin of anal lobe; Dc, dorsocentral setae; DS, dorsal seta; H, hooklets; HC, humeral callus; LLS, lateral lamellar setae; MS, median shagreen area; Pc, precorneal setae; PSA, pedes spurii A; PSB, pedes spurii B; ScuT, scutal tubercle; THB, thoracic horn base; V, total number of ventral anal lobe setae; VS, ventral setae of anal lobe; VSR, ventral spine rows.)


CT
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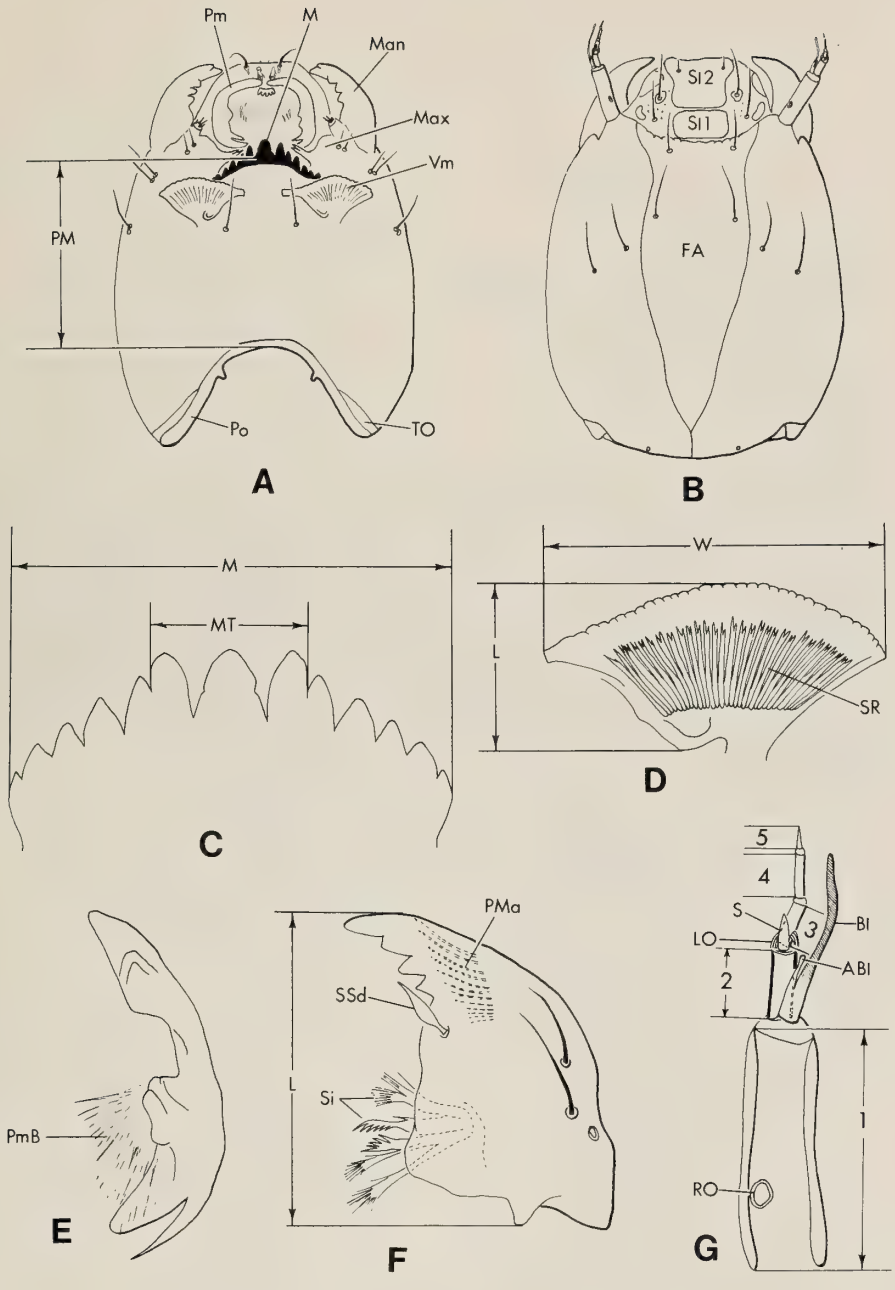
AS
MS
LLS
DS
D
VSR
PSA
CS
VS
E

FIG. 6. Larval morphology: A) Ventral view of head capsule. B) Dorsal view of head capsule. C) Mentum. D) Ventromental plate. E) Premandible. F) Mandible. G) Antenna.(ABl, accessory blade; Bl, antennal blade; FA, frontal apotome; L, length; LO, lauterborn organ; M, mentum width; Man, mandible; Max, maxilla; MT, width of median teeth; PM, postmentum length; PMa, pecten mandibularis; Pm, premandible; PmB, premandibular brush; Po, postocciput; RO, ring organ; S, style; Si, seta interna; Sl 1,2, labral sclerites 1,2; SR, strial ridges; SSd, seta subdentalis; TO, triangulum occipitale; Vm, ventromental plate; W, width.)


Pm
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PMa
SSd
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4
S
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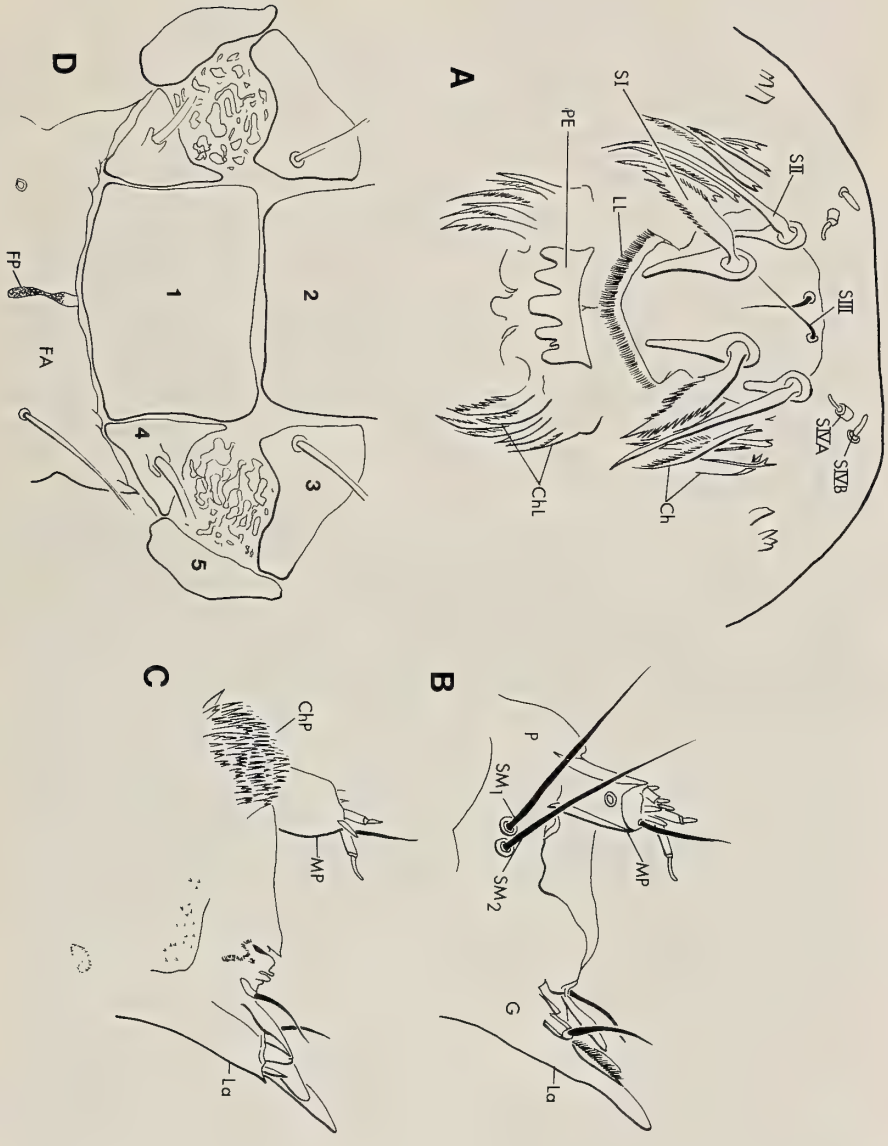
BI
LO
ABI
2
1
RO
G

FIG. 7. Larval morphology: A) Palatal surface of labrum. B) Ventral view of maxilla. C) Dorsal view of maxilla. D) Anterior portion of frontal apotome and related labral sclerites 1–5 of *D. fusconotatus*. (Ch, chaetae; ChL, chaetulae laterales; ChP, chaetulae of palpiger; FA, frontal apotome; FP, frontal process; G, galea; La, lacinia; LL, labral lamella; MP, maxillary palp; P, palpiger; PE, pecten epipharyngis; $SM_{1,2}$, setae maxillaris; SI-SIVA, SIVB, labral setae; 1-5, labral sclerites 1-5.)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ChL
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Chapter II.
A Review of the Afrotropical *Dicrotendipes* With Descriptions of the Immature Stages

This chapter presents a review of the 14 species of Afrotropical *Dicrotendipes* and describes or redescribes the immature stages of 5 species (only the pupal stage is described for *D. cordatus*).

The genus *Dicrotendipes* was originally described from the Afrotropical region (Kieffer 1913b). Freeman (1957) provided a first revision of the Afrotropical species; he included 19 species in *Chironomus* (*Dicrotendipes*), 6 of which he described as new. Freeman & Cranston (1980) provided an updated checklist. These works concentrated only on the adult stages. The immature stages had never been fully described until, in a recent revision of the western Palaearctic *Dicrotendipes,* Contreras-Lichtenberg (1986) described the immature stages of some species which are also found in the Afrotropical region; *D. fusconotatus* (larva and pupa), *D. peringueyanus* (pupa) and *D. septemmaculatus* (larva and pupa, as *D. quatuordecimpunctatus*).

A key to identify adults was provided by Freeman (1957), but one should be aware that Freeman's key included several species no longer considered to be members of *Dicrotendipes.* A new key to the adult males of Afrotropical *Dicrotendipes* is provided below. The species *chloronotus* Kieffer is now considered a *Kiefferulus* (Freeman and Cranston 1980). Freeman (1957) and Freeman and Cranston (1980) erroneously synonymized *Carteronica* Strand (= *Carteria* Kieffer) with *Dicrotendipes* (cf. also Ashe 1983). As noted by Epler (1987a), these genera are not synonymous. The Afrotropical species *crispi* Freeman, *regalis* Goetghebuer, *multispinosus* Freeman and *penicillatus* Freeman, formerly included in *Dicrotendipes,* somewhat resemble *Carteronica* in the adult stage (the species *regalis* was originally described as a *Carteria*). Although these species resemble *Carteronica,* based upon examination of the immature stages of reared *multispinosus* and immature *Chironomus longilobus* (Kieffer) (type-species for *Carteronica*), these Afrotropical species must be placed in a new genus.

At least one other described Afrotropical species, *Xenochironomus trisetosus* (Kieffer, 1922) may be a *Dicrotendipes* (see description in Freeman 1957:381). It possesses an inferior volsella similar to that of *D. bredoi.* Until reared immature stages are available, I believe it best to retain *trisetosus* in *Xenochironomus.*

The following key will replace that found in Freeman (1957:359–360). Descriptions of adults and illustrations of wings and male terminalia can be found in Freeman (1957).

Key to Adult Males of Afrotropical *Dicrotendipes*

1. Wings with spots or bands, or clouds along veins 2
   Wings immaculate 8
2. Inferior volsella simple, at most apex deeply notched 3
   Inferior volsella with apex deeply bifid 5
3. Wing with dark distal band covering or touching RM 4
   Wing with dark distal band not touching RM . . . . . *D. leucolabis* Kieffer
4. Superior volsella preapically expanded, appearing somewhat globose . . . . . *D. cordatus* Kieffer
   Superior volsella not preapically expanded . . . . . *D. collarti* (Goetghebuer)
5. Wing pattern weak, consisting of clouds along major veins . . *D. sudanicus* (Freeman)
   Wing pattern consisting of spots (which may be weak in 1 species) 6
6. Small, membranous, triangular flap-like appendages present laterad of anal point . . . . . *D. fusconotatus* (Kieffer)
   Membranous appendages near anal point absent 7
7. Wing with 6–7 well defined spots, with 1 spot usually present in cell m_{3+4} . . . . . *D. septemmaculatus* (Becker)
   Wing with weakly defined spots, none present in m_{3+4} . . . *D. peringueyanus* Kieffer
8. Base of anal point with lateral projections; apex of inferior volsella narrow, not expanded . . . . . *D. bredoi* (Goetghebuer)
   Base of anal point without lateral projections; apex of inferior volsella expanded . . 9
9. Anal point broad and strongly reflexed ventrad 10
   Anal point not as above 11
10. Superior volsella somewhat cylindrical with globose to pediform apex; apex of superior volsella with mediad membranous area bearing sensilla chaetica; foretarsi without beard . . . . . *D. kribiicola* (Kieffer)
    Superior volsella not cylindrical with globose apex, but rather leaf shaped with attenuate apex; apex of superior volsella without membranous area bearing sensilla chaetica; foretarsi bearded . . . . . *D. ealae* (Freeman)
11. Superior volsella short, globose, with medially directed apical point . . . . . *D. nigrolineatus* (Freeman)
    Superior volsella somewhat cylindrical or with elongate pedicel 12
12. Inferior volsella with large swollen apex; superior volsella with small mesally directed apical point . . . . . *D. schoutedeni* (Goetghebuer)
    Inferior volsella with normal, moderately expanded apex; superior volsella without small mesally directed apical point 13
13. Anal point long and thin, with 2–4 dorsal basal setae . *D. freemani* Epler, nom. nov.
    Anal point shorter, wider, with more than 6 dorsal basal setae . . . . . *D. chambiensis* (Goetghebuer)

Dicrotendipes bredoi (Goetghebuer)

Chironomus Bredoi Goetghebuer, 1936:473.
Chironomus (*Dicrotendipes*) *bredoi* Goetghebuer: Freeman 1957:369.
Dicrotendipes bredoi (Goetghebuer): Freeman and Cranston 1980:190; Hare & Carter 1987:70.

See adult description in Goetghebuer (1936:473) and Freeman (1957:369); the immature stages are unknown.

This is quite an unusual species for a *Dicrotendipes,* and may not belong here but in another, possibly new, genus. The superior and inferior volsellae are not typical for *Dicrotendipes.* Examination of the immature stages is needed before this species can be placed with certainty. There are no ventral accessory setae apparent on S VI. The specimen from Nigeria represents the first record for this species from that country.

MATERIAL EXAMINED: NIGERIA: Lake Opi nr Nsukka, light trap, 29-30-XII-1979, leg. L. Hare, 1 male (LH). [ZAIRE]: "Belgian Congo," Eala, X-1929, H.J. Bredo, 1 male (holotype) (KM).

Dicrotendipes chambiensis (Goetghebuer) (Fig. 8)

Chironomus (*Limnochironomus*) *chambiensis* Goetghebuer, 1936:464.
Chihronomus (*Dicrotendipes*) *chambiensis* Goetghebuer: Freeman 1957:368.
Dicrotendipes chambiensis (Goetghebuer): Freeman and Cranston 1980:190.

See adult description in Goetghebuer (1936:464) and Freeman (1957:368); the immature stages are unknown.

The superior volsella of the holotype of *D. chambiensis* (Fig. 8C) is somewhat stouter than that of *D. freemani* (Fig. 8A), and is apparently distorted from preparation procedures. Specimens from Zaire and South Africa in the BM determined as *chambiensis* have superior volsellae (Fig. 8D) which are more similar to the Nearctic *D. lucifer* complex (Epler 1987a: Figs. 111, 112), and possess numerous dorsal basal or dorsomesal setae on T IX. *D. freemani* specimens have 2–4 T IX dorsal basal setae and superior volsellae more similar to those of *D. nervosus* (Epler 1987a: Figs. 105–109). I could not discern any dorsal setae on T IX of the *D. chambiensis* holotype specimen. The Zaire and South Africa specimens might represent a new species, but without reared associations I cannot justify "splitting" the species. The differences between the anal points and inferior volsellae of *D. freemani* (as *binotatus*) and *D. chambiensis* cited by Freeman (1957:368) and utilized in the key above could be attributed to individual variation, as can the differences in the superior volsellae. It should also be noted that superior volsellae with menbranous apices, such as those possessed by *D. freemani* and *D. chambiensis,* are very sensitive to pressure induced variations caused by mounting procedures.

The hypopygium of the *D. chambiensis* holotype was mounted between 2 pieces of celluloid on the pin with the rest of the specimen and was in very poor condition. The mount had split open, the mounting medium had dried and broken the hypopygium. I remounted the hypopygium in balsam on a microscope slide and was able to salvage the gonocoxae, one superior

volsella and T IX with the anal point; the inferior volsellae and the gonostyli are lost.

MATERIAL EXAMINED: [SOUTH AFRICA]: Transvaal: Blaaubank River, IV-1957, A.D. Harrison & B.R. Allanson, 1 male (BM); Blaaubank River nr Sterkfontein, IV-1957, A.D. Harrison & B.R. Allanson, 1 male (BM). [ZAIRE]: Elizabethville, 17, 24-XII-1938, H.J. Bredo, 2 males (BM); Escpm. Kabasha: Chambi, X-1933, Dr. De Wulf, 1 male (holotype) (KM).

Dicrotendipes collarti (Goetghebuer)

Chironomus (*Dicrotendipes*) *collarti* Goetghebuer, 1936:466; Freeman 1957:366.
Dicrotendipes collarti (Goetghebuer): Freeman and Cranston 1980: 190.

See Goetghebuer (1936:466) and Freeman (1957:366) for the adult description; the immature stages are unknown. I have seen one male with 9 heavy spine-like setae on S VI.

MATERIAL EXAMINED: KENYA: Aberdare Range, Chania Falls, 4,000 feet, B.M.E. Afr. Exp., X-1934, F.W. Edwards, 1 male (BM). [ZAIRE]: "Belgian Congo": Ituri, Alokoko, 11-II-1930, A. Collart, 1 male (holotype) (KM); Katanga, Kafubu Mission, IX-1931, Miss A. Mackie, 1 male (BM).

Dicrotendipes cordatus Kieffer (Figs. 1, 9)

Dicrotendipes cordatus Kieffer, 1922:64; Freeman 1955a:22; Freeman and Cranston 1980:190; Hare & Carter 1987:70.
Paratendipes pictus Goetghebuer, 1934:199.
Chironomus (*Paratendipes*) *pictus* (Goetghebuer): Freeman 1954a: 443.
Chironomus (*Dicrotendipes*) *cordatus* (Kieffer): Freeman 1957:365; Dejoux 1968:56.

See adult description in Kieffer (1922:64) and Freeman (1957:365). There are 4–6 heavy spine-like ventral accessory setae on S VI (Fig. 1F). The holotype of *D. cordatus* is apparently lost (Freeman 1957:366).

This species is probably closely related to the Afrotropical *D. kribiicola,* the Nearctic *D. leucoscelis* and the Palaearctic *D. notatus.*

PUPA: (n = 3)

COLOR. Light brown, with darker areas along lateral margins of tergites.

LENGTH. Total 4.38–5.03, 4.64 mm. Cephalothorax 1.11–1.16, 1.13 mm. Abdomen 3.27–3.92, 3.52 mm.

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 9A). Dorsum moderately to well pebbled. Dc_2 closer to Dc_3. Thoracic horn base (Fig. 9B) with tracheal bundles narrowly joined or fused medially.

ABDOMEN (Fig. 9C). Sternites I-III with fine lateral shagreen bands; S I with posterior band; S II occasionally with anterior band. Tergite I without shagreen; T II with median quad-

rilateral shagreen area; T III-V with larger median quadrilateral shagreen area, areas extended laterally on anterior portion; T VI with Y or T shaped shagreen area; T VII with anterior band of fine shagreen and a pair of posterolateral ovoid shagreen areas; T VIII with an anterior pair of ovoid fine shagreen areas and a smaller posterior pair of ovoid shagreen areas; shagreen areas on T II-VI with spines larger in middle of area. Tergites III-V with posterior conjunctival band of fine spinules; T V posteriorly with 2 groups of intersegmental spines, 2-6 spines in each group; T VI-VIII with weak to moderate reticulate cuticular pattern posterolaterally. Posterior margin of T II with transverse row of 64-101, 84 hooklets. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Figs. 2D, E) single or multiple, small. Anal lobes with 45-54, 49 setae. DR 2.76–3.16, 2.92.

MATERIAL EXAMINED: NIGERIA: Lake Opi nr Nsukka, 14-27-I-1979, leg. Landis Hare, 1 male, 1 female/Pex, 2 Pex (LH). Kafanchan, 6-V-1979, J.C. Deeming, 1 male (BM). SUDAN: Khartoum, at light, XI-1951, D.J. Lewis, 3 males (BM). Liednum nr Wau, 13-IV-1955, E.T.M. Reid, 1 male (BM). UGANDA: Lake Nabugabo, 13-XI-1934, F.W. Edwards, 1 male (BM).

Dicrotendipes ealae (Freeman)

Chironomus (*Dicrotendipes*) *ealae* Freeman, 1957:369; Dejoux 1968:57.
Dicrotendipes ealae (Freeman): Freeman and Cranston 1980:190.

See adult description in Freeman (1957:369); the immature stages are unknown. There are no ventral accessory setae apparent on S VI.

MATERIAL EXAMINED: S[OUTH] A[FRICA].: Natal: Howick Falls, 6-IV-1953, G.H. Satchell, 2 males (holotype, paratype) (BM).

Dicrotendipes freemani nom. nov. (Fig. 8)

Chironomus binotatus Kieffer, 1911b:354 (junior homonym of *Ch. binotatus* Wiedemann, 1817).
Chironomus seychelleanus Kieffer, 1911b:356 (part) (junior synonym of *Chironomus callichirus* Kieffer, 1911b); (part) = *Ch. binotatus* Kieffer, 1911b.
Chironomus (*Dicrotendipes*) *binotatus* Kieffer: Freeman 1957:367.
Dicrotendipes binotatus (Kieffer): Freeman and Cranston 1980:190.

See Freeman (1957) for the description of the adult; the immature stages are unknown.

Chironomus seychelleanus was described from a male and a female (Kieffer 1911b). Freeman (1957:341, 367) found that the male was a *Ch. callichirus* Kieffer and the female a *D. binotatus.* I have examined Kieffer's female specimen; it is a *Dicrotendipes* and has at least 2 ventral accessory setae on S VI. It matches the holotype male of *Ch. binotatus,* which I also examined, in coloration, and probably is the female of this species. Freeman (1957:341) fixed the male specimen of *Ch. seychelleanus* as the lectotype; by page priority he considered it a junior synonym of *Ch. callichirus.* He

(Freeman 1957:368) listed the female as a "cotype"; it automatically became a paralectotype of *Ch. seychelleanus* (ICZN, Art. 73(b)(ii)). Because *Ch. binotatus* Kieffer, 1911 is a junior homonym of *Ch. binotatus* Wiedemann, 1817 (now considered the type-species of *Krenopelopia* Fittkau; see Fittkau 1962:262), and *Ch. seychelleanus* Kieffer is not available for this species, a new name must be given this species. I am happy to name this species for Dr. Paul Freeman, in recognition for the work he has done on the African chironomid fauna.

Dicrotendipes freemani is very similar to *D. chambiensis* (Goetghebuer). These may be the same species, but without a comparison of the immature stages of the 2 species I cannot consider synonymizing them.

The superior volsella of this species (Figs. 8A, B) also resembles that of the Holarctic *D. nervosus* (Staeger) and/or the Indo-Pacific *D. flexus* (Johannsen). Again, reared specimens are needed to confirm species relationships. See also remarks under *D. chambiensis.*

MATERIAL EXAMINED: ETHIOPIA: Bahar Dar, Tana-See, 26-I-1977, 1 male (ZS). [SEYCHELLES ISLANDS]: La Reunion: St. Pierre Villa, 5-I-1956, J.Hamon, 1 male (BM); Mahé, '08-9, Seychelles Exp., 1 male, 1 female (holotype male of *binotatus* and paralectotype female of *seychelleanus*) (BM) (Kieffer (1911b) lists the locality data for both specimens as: "Seychellen, Mahé: marshes on coastal plain at Anse aux Pins and Anse Royal, 19-21-I-1909.")

Dicrotendipes fusconotatus (Kieffer) (Fig. 10)

[?] *Dicrotendipes trilabis* Kieffer, 1922:63.
Calochironomus fusconotatum Kieffer, 1922:68.
Calochironomus griseonotatus Kieffer, 1922:69.
Calochironomus griseosparsus Kieffer, 1922:69.
Dicrotendipes forficula Kieffer, 1925:298.
Dicrotendipes nilicola Kieffer. 1925:300.
Polypedilum quatuorpunctatum Goetghebuer, 1936:489.
Dicrotendipes fusconotatus (Kieffer): Freeman 1955a:22; Dejoux 1977:293; Freeman and Cranston 1980:190; Reiss 1986:159; Contreras-Lichtenberg 1986:717.
Chironomus (*Dicrotendipes*) *fusconotatus* (Kieffer): Freeman 1957:362; Dejoux 1968:56.

See adult description in Freeman (1957:362) and Contreras-Lichtenberg (1986:718). There are no ventral accessory setae apparent on S VI. Contreras-Lichtenberg (1986) also described the pupa and larva of *D. fusconotatus.* I cannot reliably distinguish the pupa of *D. fusconotatus* from *D. pallidicornis* Goetghebuer, *D. peringueyanus* (as described by Contreras-Lichtenberg 1986) or *D. sudanicus.* Characters given in couplets 7 and 8 of Contreras-Lichtenberg's (1986) pupal key will not separate these species (the number of T II hooklets given for *D. fusconotatus* is very low; see description below); see also remarks under *D. peringueyanus* below.

I follow Freeman (1957) in listing *D. trilabis* as a probable synonym; the type is apparently lost and the description of the species appears to be that of a teneral *D. fusconotatus*. Kieffer described *fusconotatus* as 4 different species in one paper (Kieffer 1922) and as 2 more species in a later paper (Kieffer 1925).

PUPA: (n = 4)

COLOR. Very light brown, with light brown along lateral margins of tergites.

LENGTH. Total 4.08–4.90 mm (2).Cephalothorax 0.95–1.20 mm (2). Abdomen 3.13–3.69 mm (2).

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 10A). Dorsum moderately to well pebbled. Dc_2 closer to Dc_3. Thoracic horn base (Fig. 10B) with tracheal bundles separate.

ABDOMEN (Fig. 10C). Sternites II-III with fine lateral shagreen bands; also fine spinules scattered over S II-III; T I with posterolateral weak to well-developed reticulate pattern; T II with median quadrilateral shagreen area; T III-V with larger median quadrilateral shagreen area, areas somewhat extended laterally on anterior and/or posterior portion; T VI with V shaped shagreen area; T VII with an anterior pair of suboval shagreen areas; T VIII with a pair of longitudinal bands of fine shagreen; shagreen areas of T II-VI with spines larger in middle and posterior portion of area. Weak shagreen present dorsally on anal lobe. Tergites III-V with posterior conjunctival band of fine spinules; T VI-VIII with well developed reticulate cuticular pattern posterolaterally. Posterior margin of T II with transverse row of 59–68, 58 hooklets (40 in Contreras-Lichtenberg (1986)). T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Figs. 10D, E) single or multiple, very small. Anal lobes with 61–78 setae (3), partially biserial. DR 2.35–2.64 (3).

FOURTH INSTAR LARVA: (n = 7)

COLOR. Head capsule light brown to brown, mentum and mandibular apodemes darker, sometimes with darker area anterior to postocciput; postocciput dark brown-black.

HEAD. Postmentum length 215–253, 234 (6). Mandible (Figs. 10F, G) length 203–223, 212 (6), with second and third lateral teeth partially fused, a shallow to deep incision proximal to these, followed by a fourth lateral tooth or "hump"; 2 well developed dorsal teeth present. Pecten mandibularis composed of 11–15, 12 (6) setae. Mentum (Fig. 10H) with 13 teeth, 5th and 6th teeth fused or closely appressed; width 133–143, 139 (6); MR 2.51–2.64, 2.59 (6). Ventromental plate with crenulate anterior margin; width 99–106, 103 (6); length 40–50, 45. VPR 2.10–2.50, 2.30 (6); IPD 72–79, 75 (6); PSR 1.27–1.44, 1.37 (6); 20–22, 21 strial ridges. Length of antennal segments: 64–79, 69 (5); 16–19, 18 (4); 11–12, 11 (5); 12–14, 13 (5); 6–7, 6 (5). AR 1.28–1.49, 1.40 (4) (Fig. 10I). Inner blade of premandible (Fig. 10J) greater than outer blade. Pecten epipharyngis (Fig. 10K) with 3–5, 5 (6) lobes. Anterior margin of frontal apotome (Fig. 7D) with long, thin ventral frontal process; labral sclerite 1 smooth. S I with 6–9, 7 fringes (Fig. 10L).

BODY. Ventral tubuli absent.

MATERIAL EXAMINED: "CONGO BELGE": Ishango bae, 20-II-1954, J. Verbeke—KEA, 1 male (BM); P.N.A. Vitshumbi (S. Lac. Ed.), 12-14-I-1953, J. Verbeke–KEA, 4 males (BM). EGYPT: Lake Nasser, El Madin, 7-XI-1971, M. Gillies, 1 male (BM); Lake Nasser, Nubia, 9-11-I-1981, P.S. Cranston, 2 males (BM). KENYA: Lake Beringo, Yellow Kay, XII-1977, Waddesdon School Exp., 1 female (BM). SUDAN: Abu Hamed, March 1948, 1 male (US). Blue Nile, Ummbenane nr Singa, light trap, 19-IV-1981, P. Mellor, 1 male (BM). Khartoum, 24-I-1953, D.J. Lewis, 2 males (BM). Wad Medani, Feb. 1952, D.J. Lewis, 1 male (BM). White Nile, Kalakla, 20 km S Khartoum, to light, I-1980, P.S. Cranston, 4 males, 1 female (BM). White Nile, Jebel Aulia, I-1980, P.S. Cranston, 1 male/Pex/Lex, 1 pharate male pupa/Lex, 2 males, 1 female/Pex 1 pharate female pupa, 5 larvae (BM).

Dicrotendipes kribiicola (Kieffer) (Fig. 11)

Phytochironomus kribiicola Kieffer, 1923:152.
Chironomus (*Dicrotendipes*) *kribiicola* (Kieffer): Freeman 1957:368; Dejoux 1968:57.
Dicrotendipes kribiicola (Kieffer): Freeman and Cranston 1980:190; Hare & Carter 1987:70.

See adult description in Freeman (1957:368), the type is apparently lost. There are 4–5 ventral accessory setae on S VI.

Freeman and Cranston (1980:190) erroneously listed *Polypedilum* as the genus in which this species was originally placed. The record from Nigeria is the first record of this species from that country.

I also examined a male specimen from Lake Kainji in Nigeria (in the BM collection) which superficially resembles *D. kribiicola,* differing mainly in the shape of the superior volsella. This specimen may represent a new species, but is in too poor condition to allow sufficient description.

PUPA: (n = 7)

COLOR. Light brown, with darker areas along lateral margins of tergites.

LENGTH. Total 3.92 mm (1). Cephalothorax 0.94—0.96 mm (2). Abdomen 2.70–3.17, 2.96 mm (5).

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 5A), 40–53, 49 (3) high, 60–105, 88 (3) wide. Dorsum moderately pebbled. Dc_2 closer to Dc_3. Thoracic horn base (Fig. 5B) with tracheal bundles fused medially or very closely appressed.

ABDOMEN (Fig. 11C). Sternites I-III with fine shagreen. Tergite I sometimes with weak lateral shagreen areas; T II-V with median quadrilateral shagreen area; T VI with a pair of median triangular shagreen areas, areas sometimes narrowly joined; T VII with anterior band of fine shagreen or a pair of anterolateral ovoid shagreen areas; T VIII with an anterior pair of ovoid fine shagreen areas and a smaller posterior pair of ovoid shagreen areas of these two areas joined in a pair of lateral bands; shagreen areas on T II-VI with spines larger in middle of area. Tergites III-V or IV-V with posterior conjunctival band of fine spinules; T V posteriorly with 2 groups of intersegmental spines, 2–4 spines in each group. Posterior margin of T II with transverse row of 52–68, 63 hooklets. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Fig. 11D) single or multiple, small to thorn-shaped. Anal lobes with 28–39, 36 setae. DR 1.50–2.41, 1.83.

FOURTH INSTAR LARVA: (n = 4)

COLOR. Head capsule light yellow-brown, postmentum darker brown; postocciput, mentum and mandibular apodemes dark red-brown.

HEAD. Postmentum length 180–195, 190 (3). Mandible (Fig. 11E) length 157–165, 160 with 3 lateral teeth; 2 well-developed dorsal teeth present. Pecten mandibularis composed of 9–10, 9 setae. Mentum (Fig. 11F) with apparently only 11 teeth, 5th and 6th teeth fused, 4th closely appressed; width 105–115, 110 (3); MR 2.10–2.20, 2.16 (3). Ventromental plate with smooth anterior margin; width 78–85, 83; length 38–43, 42. VPR 1.81–2.24, 1.99; IPD 41–45, 43 (3); PSR 1.81–2.07, 1.91 (3); 24–28, 25 strial ridges. Length of antennal segments: 54–61, 57; 18–20, 19; 9–10, 9 (3); 12–14, 13 (3); 4–5, 5 (3). AR 1.17–1.29, 1.23 (3) (Fig. 11G). Inner blade of premandible (Fig. 11H) subequal to outer blade. Pecten epipharyngis (Fig. 11I) with 5 lobes. Frontal apotome (Fig. 11J) with large ventral mesal ovoid pit; labral sclerite 1 smooth, reduced, much broader than long. S I with 6–9 (2) fringes.

BODY. Ventral tubuli absent.

MATERIAL EXAMINED: GHANA: Accra, J.D. Thomas, 12 males (BM). NIGERIA: Lake Opi nr Nsukka, mass rearing, 16-22-X-1977, leg. L. Hare, 1 male/Pex, 1 Pex; same locality, light trap, 31-XII-1978–1-I-1979, leg. L. Hare, 1 male (LH); same locality, mass rearing, 14-25-I-1979, leg. L. Hare, 2 males/Pex (LH); same locality, 28-I-3-II-1979, leg. L. Hare, 1 female/Pex/Lex (LH); same locality, 10-11-III-1979, leg. L. Hare, 1 female/Pex/Lex (LH); same locality, 22-IV-1979, leg. L. Hare, 3 larvae (LH); same locality, emergence trap, 24-25-XI-1979, leg. L. Hare, 1 male/Pex (LH). [ZAIRE]: "Congo Belge," Eala, I-1935, J. Ghesquiere, 1 male (BM).

Dicrotendipes leucolabis Kieffer

Dicrotendipes leucolabis Kieffer, 1922:65; Freeman and Cranston 1980:190.
Polypedilum (?) *aequatoris* Goetghebuer, 1936:482.
Chironomus (*Dicrotendipes*) *leucolabis* (Kieffer): Freeman 1957:367.

See adult descriptions in Kieffer (1922:65), Goetghebuer (1936:482) and Freeman (1957:367); immature stages are unknown.

This species may be a senior synonym of *D. collarti.* However, the type of *leucolabis* is probably lost and Kieffer's figure (1922: Fig. 67) of the hypopygium is insufficiently clear. Freeman (1957) synonymized *Polypedilum aequatoris,* known only as a female, with this species on the basis of wing maculation and body coloration. Kieffer's (1922) description of the wing of *D. leucolabis* does seem to match that illustrated for the female *aequatoris* specimen (Goetghebuer 1936:Fig. 35). The wing pattern of *leucolabis* differs from that of *collarti:* the transverse band is adjacent to RM and FCu in *collarti* and more distal in *leucolabis;* also the quadrate spot over the anal vein is smaller in *collarti.* These differences may be variations within one species; reared associations would have to be examined to determine whether 1 or 2 species are present.

Goetghebuer (1936) was apparently unsure of the generic position of this species, which he denoted with a parenthetical question mark following the genus name; Freeman examined the type and considered it a *Dicrotendipes* on the basis of tibial spurs. I have not seen any specimens of *D. leucolabis.*

Dicrotendipes nigrolineatus (Freeman)

Chironomus (*Dicrotendipes*) *nigrolineatus* Freeman, 1957:370.
Dicrotendipes nigrolineatus (Freeman): Freeman and Cranston 1980:190.

See adult description in Freeman (1957:370); immature stages are unknown. This species may be an *Einfeldia;* examination of reared immature stages is necessary for correct placement. There are no ventral accessory setae apparent on S VI.

MATERIAL EXAMINED: [ZAIRE]: "Belgian Congo": Elisabethville, 17-31-XII-1932, C. Seydel, 3 females (paratypes) (BM); same locality & collector, II-1933, 1 female (paratype) (BM); same locality & collector, 1-12-III-1933, 1 male (holotype) (BM).

Dicrotendipes peringueyanus Kieffer

Dicrotendipes peringueyanus Kieffer, 1924:257; Freeman 1955b:372; Disney 1975; Reiss 1977b:91, 93; Freeman and Cranston 1980:190; Prat 1981:58; Contreras-Lichtenberg 1986:706.
Polypedilum griseovittatum Goetghebuer, 1936:485.
Chironomus (*Dicrotendipes*) *peringueyanus* (Kieffer): Freeman 1957:364; Dejoux 1968:57.

See adult description in Freeman (1957:364) and Contreras-Lichtenberg (1986:707); the pupa has been described by Contreras-Lichtenberg (1986:706); the larva is unknown. There were no ventral accessory setae present on the males I examined.

This species may be a variant of *D. fusconotatus.* The genitalia are similar and the 2 species differ only slightly in wing maculation (see Freeman 1957). Without associated larval stages a decision regarding the status of the 2 species cannot be made.

Disney (1975) reported the phoretic association of the immature stages of *D. peringueyanus* with the African river crabs *Potomanautes africanus* (A. Milne-Edwards) and *P. pobeguini* (Rathbun) in Cameroon. The chironomid identifications were based on larvae reared to adults. Disney placed this material in the BM (Disney, pers. comm.). However, this material could not be located recently (Cranston, pers. comm.).

The pupa of *D.peringueyanus* as described by Contreras-Lichtenberg (1986) is not separable from *D. fusconotatus, D. pallidicornis* or *D. sudanicus.* In her pupal key, Contreras-Lichtenberg (1986) separates *D. perigueyanus* from *D. pallidicornis* based on the absence of conjunctival spinules on *D. pallidicornis.* However, all specimens of *D. pallidicornis* which I have examined do possess these spinules.

MATERIAL EXAMINED: [CAMEROON]: Kumba, Mambonjese, [on] crab *P. africanus,* 13-V-1969, [Disney], 1 male hypopygium & leg, det. A.D. Harrison (BM). [SOUTH AFRICA]: Cape Prov: Upington, XI-1950, P. Brinck, 2 males (BM); Transvaal: Nelspruit, XI-1956-II-1957, G.H. Frank, 1 male (BM).

Dicrotendipes schoutedeni (Goetghebuer)

Chironomus (*Limnochironomus*) *Schoutedeni* Goetghebuer, 1936:465.
Chironomus (*Dicrotendipes*) *schoutedeni* Goetghebuer: Freeman 1957:370; Freeman 1961b:247.
Dicrotendipes schoutedeni (Goetghebuer): Freeman and Cranston 1980:190; Hare & Carter 1987:70.

See adult descriptions in Goetghebuer (1936:465) and Freeman (1957:370); the immature stages are unknown. The anal tergal bands are unusual for a *Dicrotendipes;* there are no apparent ventral accessory setae on S VI. I have not examined the holotype.

MATERIAL EXAMINED: [BENIN] "DAHOMEY": cercle de Porto Novo, GBE home, 7-12-54, J. Hamon, 1 male (BM). NIGERIA: Lake Kainji, A. Bidwell, 1 male (BM); Lake Opi nr Nsukka, light trap, 13-14-I-1979, leg. L. Hare, 1 male (LH).

Dicrotendipes septemmaculatus (Becker) (Figs. 12, 49)

Chironomus septemmaculatus Becker, 1908:77.
[?] *Chironomus* (*Prochironomus*) *punctatipennis* Kieffer, 1910:234. **NEW SYNONYMY.**
Dicrotendipes pictipennis Kieffer, 1913b:23; Freeman 1955a:22.
[?] *Tendipes punctatipennis* (Kieffer): Kieffer 1913a:138.
Dicrotendipes pilosimanus Kieffer, 1914:262; Freeman 1955b:372; Sublette and Sublette 1973:404; Reiss 1977b:93; Reiss 1978:75; Freeman and Cranston 1980:190; Reiss 1986:159; Contreras-Lichtenberg 1986:716; Chaudhuri & Guha 1987:27.
Dicrotendipes formosanus Kieffer, 1916:115; Sublette and Sublette 1973:403; Hashimoto et al. 1981:12; Sasa and Hasegawa 1983:320. **NEW SYNONYMY.**
Dicrotendipes formosanus var *frontalis* Kieffer, 1916:116.
Dicrotendipes speciosus Kieffer, 1924:256; Kieffer 1925:299.
Stictochironomus sexnotatus Goetghebuer, 1930:95.
Chironomus hirtitarsis Johannsen, 1932:534; Sublette and Sublette 1973:402. **NEW SYNONYMY.**
Polypedilum quatuordecimpunctatum Goetghebuer, 1936:48.
Dicranotendipes speciosus Kieffer: Kruseman 1949:254 (misspelling).
Chironomus (*Dicrotendipes*) *pilosimanus* (Kieffer): Freeman 1954b:19; Freeman 1957:360; Freeman 1961a:247; Freeman 1961b:694; Dejoux 1968:56 (misspelled as *pilosinamus*).
Chironomus (*Dicrotendipes*) *pilosimanus* subsp. *quatuordecimpunctatus* (Goetghebuer): Freeman 1957:361.
Dicrotendipes frontalis Kieffer: Sublette and Sublette 1973:403. **NEW SYNONYMY.**
[?] *Dicrotendipes punctatipennis* (Kieffer): Sublette and Sublette 1973:404; Chaudhuri & Guha 1987:27 (misspelled as *punctipennis*).
Dicrotendipes rajasthani Singh and Kulshrestha, 1977:233. **NEW SYNONYMY.**
Dicrotendipes hiritarsis (Johannsen): Guha et al. 1982:30; Chaudhuri & Guha 1987:27 (misspelling).
Dicrotendipes quatuordecimpunctatus (Goetghebuer): Contreras-Lichtenberg 1986:710. **NEW SYNONYMY.**
Dicrotendipes septemmaculatus (Becker): Cranston and Armitage 1988.

See adult descriptions in Freeman (1957:360; 1961b:694; as *pilosimanus*) and Contreras-Lichtenberg (1986:711, 716, as *pilosimanus* and *quatuordecimpunctatus*). There are no ventral accessory setae apparent on S VI.

Dicrotendipes septemmaculatus is one of the most widely distributed members of this genus in the world (Fig. 49). I have examined reared material from the Afrotropical, southern Palaearctic (Lebanon) and Australian

regions. Afrotropical pupae possess long, well developed cephalic tubercles; in the one reared Australian pupa examined, the cephalic tubercles are not as well developed. Cephalic tubercle length often varies greatly within species in other species of *Dicrotendipes*. Pupae of *D. septemmaculatus* are difficult to separate from *D. fusconotatus, D. pallidicornis, D. peringueyanus* and *D. sudanicus*. Shagreen patterns in all 5 species are similar, and T II hooklet counts and anal lobe setal numbers overlap. *Dicrotendipes septemmaculatus* possesses a relatively well developed humeral comb or ridge; however, the development of this structure varies intraspecifically. It is also present, although more weakly developed, in *D. fusconotatus* and *D. sudanicus*. In *D. septemmaculatus* and *D. sudanicus,* Dc_2 is closer to Dc_1 than to Dc_3; however, *D. septemmaculatus* generally is larger, possesses long, well developed cephalic tubercles (shorter, squatter in *D. sudanicus*) and generally has more anal lobe setae. I would consider specific identification of isolated pupal exuviae of these 5 species to be risky.

Wing spots are variable in *D. septemmaculatus*. They may be absent in teneral specimens, and the pair of spots in cell r_{4+5} is sometimes combined into one spot.

Based on Afrotropical material, Freeman (1957) considered *D. pilosimanus* (= *D. septemmaculatus*) to consist of 2 geographical subspecies, *D. p. pilosimanus* and *D. p. quatuordecimpunctatus* (Goetghebuer). These differ only in the presence (*D. p. pilosimanus*) or absence (*D. p. quatuordecimpunctatus*) of a fore metatarsal beard, and, as Freeman (1957) noted, intermediates occur. In all reared material made available to me for this study, the adults possessed a sparse to moderately developed beard on fore ta_2 and ta_3. The moderately developed beard on many specimens was at least as well developed as that on specimens in the British Museum collection determined as *D. p. pilosimanus*. Although some workers believe 2 species may be present, until more reared material of both "subspecies" is made available, I see little need to continue the usage of *quatuordecimpunctatus*. Fortunately, the discovery of the Becker type of *septemmaculatus* no longer necessitates the usage of the name *pilosimanus* and its subspecies (Cranston & Armitage 1988). I have examined the Becker female holotype specimen.

Cranston & Armitage (1988) also rediscovered the type of *Stictochironomus sexnotatus* Goetghebuer and considered the species to be a junior synonym of *D. septemmaculatus*. I have also examined the male lectotype specimen and concur.

I have listed *Ch. punctatipennis* Kieffer as a probable synonym of *septemmaculatus*. Kieffer's (1910) original description of *punctatipennis* lacked illustrations and for the most part described wing maculation. In a later redescription based on additional specimens, Kieffer (1913a) provided an

illustration of the hypopygium and more morphological details. In the second description (plate XI, Fig. 10, mislabeled as *Tendipes punctatissimus*), Kieffer stated (and illustrated) that the male of *punctatipennis* possessed 3 volsellae. Kieffer may have been mistaking the proximal arm of the deeply bifid inferior volsella (as in *septemmaculatus*) for a third volsella. However, without examining a male from this series, or the type series (if one exists), I can not be positive that Kieffer may have made such a mistake.

Some of the material redescribed as *Ch. punctatipennis* by Kieffer (1913a) came from the collection of E. Brunetti; Brunetti's collection is now with the British Museum. I examined 3 female specimens from Bosundhur (Bangladesh), leg. J.T. Jenkins, from that collection. Two are labeled "*Tendipes punctatipennis*" in what appears to be Kieffer's hand-writing; the third is labeled "*Chiron. punctatipennis* Kieffer." These females are to me inseparable from *D. septemmaculatus.*

The type or type series (if one exists) of *D. punctatipennis* and perhaps *D. semiviridis* (Kieffer, 1911) may be with the Zoological Survey of India, Calcutta. According to Dr. M. Datta, Zoological Survey of India (pers. comm., 12 Sept. 1986), specimens of *punctatipennis* (and *semiviridis*) are present in the collection, but "are in extremely miserable condition and are suggestive of not being mailed to anybody so as to save from further deterioration." Obviously, an on-site examination of these specimens by a competent chironomid worker will be necessary to clear up the taxonomy of *D. punctatipennis.*

I consider *D. formosanus* Kieffer to be a junior synonym of *D. septemmaculatus;* only minor differences in coloration had separated the 2 species, which I do not consider to be sufficient reason to maintain the separation. The type of *formosanus* was apparently destroyed in the 1956 fire at the Hungarian National Museum.

Hashimoto et al. (1981:12) designated a holotype and paratypes for *formosanus* from Thailand material. These designations are invalid (ICZN, Chapter XVI); holotypes and paratypes can not be designated by any other than the original author. Lectotypes and paralectotypes can not be designated from Thailand material either, because such types can only be designated from the original series. Perhaps a neotype could be designated, but because Hashimoto et al. (1981) is not a revisory work, such a designation could also be considered invalid.

PUPA: (n = 6)

COLOR. Light yellow-brown, with light brown along lateral margins of tergites.

LENGTH. Total 5.90–6.14, 5.98 mm (3). Cephalothorax 1.30–1.50, 1.41 mm (3). Abdomen 4.23–4.71, 4.49 mm (5).

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 6A), 210–250, 228 (3) high, 125–162, 139 (3) wide. Dorsum and frontal apotome moderately to well pebbled. Dc_2 closer

to Dc_1. Thoracic horn base (Fig. 6B) with tracheal bundles separate. Dorsal portion of humeral callus usually with moderately developed "comb" or ridge.

ABDOMEN. Similar to *D. fusconotatus* (Fig. 10C). Sternite I sometimes with very fine median shagreen spinules; sternites II-III with fine lateral shagreen bands; also fine spinules scattered over S II-III; Tergite I with posterolateral weak reticulate pattern; T II with median quadrilateral shagreen area; T III-V with larger median quadrilateral shagreen area, areas somewhat extended laterally on anterior and/or posterior portion; T VI with broadly V shaped shagreen area; T VII with an anterior pair of suboval shagreen areas, sometimes joined medially; T VIII with a pair of longitudinal bands of fine shagreen; shagreen areas on T II-VI with spines larger in middle and posterior portion of area. Well developed shagreen area present dorsally on anal lobe. Tergites III-V with posterior conjunctival band of fine spinules; T V-VIII with reticulate cuticular pattern posterolaterally, well developed on T VI-VIII. Posterior margin of T II with transverse row of 66–93, 79 hooklets. T VIII with 5 lateral setae. Caudolateral spurs on T VIII single or multiple, small (similar to *D. fusconotatus,* Figs. 10D, E). Anal lobes with 47–67, 57 setae, partially biserial. DR 2.25–3.03, 2.63.

FOURTH INSTAR LARVA: (n = 4)

COLOR. Head capsule light brown to brown, mentum and postocciput red-brown, with slight caudal darkening of postmentum.

HEAD. Postmentum length 240–253, 245. Mandible (Fig. 12C) length 220–240, 230, with three lateral teeth; 2 well developed dorsal teeth present. Pecten mandibularis composed of 10–12, 11 setae, apical seta very broad. Mentum (Fig. 12D) with 13 teeth, 1st and 2nd teeth fused or closely appressed; width 150–162, 153; MR 2.58–2.88, 2.71. Ventromental plate with mostly smooth anterior margin, sometimes with extremely shallow crenulations; width 100–109, 104; length 52–65, 55. VPR 1.72–2.04, 1.88; IPD 63–72, 67; PSR 1.47–1.63, 1.55; 27–29, 28 strial ridges. Length of antennal segments: 79–87, 84; 25–27, 26; 12; 15–18, 17; 6. AR 1.32–1.43, 1.39 (Fig. 12E). Inner blade of premandible (Fig. 12F) greater than outer blade. Pecten epipharyngis (Fig. 12G) with 5 lobes. Anterior margin of frontal apotome (Fig. 12H) with long, thin ventral frontal process; labral sclerite 1 smooth. S I with 8–10 (2) fringes.

BODY. Ventral tubuli absent.

MATERIAL EXAMINED: ALGERIA: Oued Bechar, 26-III-1955, leg. E.J. Fittkau, 1 male/Pex/Lex, 3 Pex (ZS). AUSTRALIA: New South Wales: Deniliquin, from egg mass #6, 6-I-1969, 1 male (JM). Northern Territory: Fogg Dam, 15 km NE Humpty Doo, at UV light, 5-X-1982, leg. J.K. Balciunas, J. Gillett, 5 males, 1 female (JB). Queensland: Charleville, light trap, 17-II-1969, leg. A.L. Dyce, 1 male (JM); Sandgate, 14-V-1974, leg. J. Martin, 1 male/Pex (JM); Somerset Dam edge, 80 mi N Brisbane, 8-VI-1968, leg. J. Martin, 1 male (JM). [BANGLADESH]: Khulna, Bosondhur, Ganges delta, on launch, 29-VII-1909, J.T. Jenkins, 3 females (BM) (*punctatipennis* specimens). BURMA: Shan State, Lnle Marsh, ½ mi N of Shwevanpye, on *Hydrilla,* 26-VI-1982, leg. J.K. Balciunas, 2 larvae (JB). CANARY ISLANDS: Tenerife, Puerto Orotava, "51307.8," 1 female (holotype of *Ch. septemmaculatus* Becker) (ZH). EGYPT: Luxor, 12-I-1981, leg. P.S. Cranston, 1 male (BM). INDIA: Karnataka: Bangalore, 20 May 1982, leg. J.K. Balciunas, M.C. Minno, 1 pharate female pupa (JB); Dasappaddodi Pond, 35.5 km WSW Bangalore, at UV light, 24-V-1982, leg. J.K. Balciunas, M.C. Minno, 1 female (JB); Medahalli Well, 15 km E of Bangalore, at UV light, 21-V-1982, leg. J.K. Balciunas, M.C. Minno, 3 males (JB); Nandi Hills, el. 1200 m, 5 Oct 1985, leg. C.W. & L.B. O'Brien, 1 male (FS). Kerala: Chalakuby, 32 km S Trichur, 10-X-1985, leg. C.W. & L.B. O'Brien, 1 male (FS). Mahar: Rahuri, Mula River, Oct. 17, 1985, leg. C.W. & L.B. O'Brien, 1 male (FS). West Bengal: Burdwan, 7-VII-1978, leg. S.K. Nandi, 1 male (BM); Malda, 4-IV-1975, 1 female (BM). INDONESIA: Java: Central Java, Jombor Lake, 10 km S Klaten, on *Hydrilla,* 28 Aug 1981, leg. J.K. Balciunas, 1 larva (JB). South Sulawesi: Lake Lampulung,

5 km NE Seng Kang, on *Hydrilla,* 3-IX-1982, leg. J.K. Balciunas, 1 larva (JB); same data, except at black light, 65 males (JB). Sumatra: Bay of Meat, Lake Toba, 10-IV-1929, 1 male (minus wing, hypopygium) (paratype *Ch. hirtitarsis*) (BM). ISRAEL: Beth Netufa, Sept 1968, leg. J. Kugler, 1 male (JM). JAPAN: Hamamatsu City, Sept–Nov. 1984, leg. H. Hashimoto, 3 males, 5 females (HH). LEBANON: Ammik, el. 850 m, 16-V-1982, leg. Z. Moubayed, 4 males, 2 females, 3 Pex (ZM); Baalbek, el. 1150 m, 18-X-1982, leg. Z. Moubayed, 1 male, 1 pharate male pupa, 1 pharate female pupa, 13 Pex (ZM); River Litani at Jib-Jennine, 1 female, 1 pharate female pupa, 8 Pex, 4 larvae (ZM). MALAGASY: Pr. Tanan, Ankeniheny River (28 °C) 4 km S Manjakatompo Forest Sta., 1-XI-71, G.F. & C.H. Edmunds, F. Emmanuel, 2 males (FS). MALAYSIA: Penang State: irrigation canal in Balik Pulau Village, on *Hydrilla,* Sept 7 1983, leg. J.K. Balciunas, 1 larva (JB). [NAMIBIA]: "S.W. AFRICA": Swakopmund, 26-30-I-1972, Southern African Exp., 2 males (BM). NIGERIA: Jos., 24-XI-1970, J.C. Deeming, 1 male, 2 females (BM). [SOUTH AFRICA]: Transvaal: Olifantsvlei, nr Johannesburg, 22-IX-54, A.D. Harrison, 1 male (BM); Jukskei River, nr Johannesburg, VII-1956, A.D. Harrison & B.R. Allansen, 1 male (BM). SPAIN: Algeciras, 1 male (lectotype of *Stictochironomus sexnotatus* Goetghebuer) (NM). SRI LANKA: 1975, leg. F. Schiemer, 1 male (ZS). [SUDAN]: W. Darfur: N. Jebel Murra, Kurra, 5600 ft, 4-VII-1932, M. Steele, 1 male (BM). UGANDA: L. Victoria, 21-VI-1950, W.W. Macdonald, 1 male (BM). YEMEN: San'a, ca. 7900 ft., at night, 10-15-X-1937, C. Rathjens, 1 male (BM). [ZIMBABWE] "N. RHODESIA": Salisbury, V-1956, E.T.M. Reid, 1 male (BM). [ZAIRE]: Elizabethville, XI-1933, C. Seydel, 1 male (BM); Elizabethville, 17-XII-1938, H.J. Bredo, 1 female (BM).

Dicrotendipes sudanicus (Freeman) (Fig. 12)

Chironomus (*Dicrotendipes*) *sudanicus* Freeman, 1957:365; Dejoux 1968:56.
Dicrotendipes sudanicus (Freeman): Dejoux 1977:294; Freeman and Cranston 1980:190; Dejoux 1984:161; Hare & Carter 1987:70.

See adult description in Freeman (1957:365). There are no ventral accessory setae apparent on S VI.

This species appears to be a diminutive *D. fusconotatus.* The hypopygia of the 2 species are basically identical. The adults of the species differ only in relative size and in wing maculation; the wing markings of *sudanicus* are "clouds" along and over the veins while *fusconotatus* possesses spots in the cells. The pupae differ slightly. The pupa of *fusconotatus* is larger, has more anal lobe setae (61–78) and Dc_2 is closer to Dc_3. The pupa of *sudanicus* is smaller, has fewer anal lobe setae (35–47) and Dc_2 is closer to Dc_1. The larval mentum of *D. sudanicus* is similar to *D. septemmaculatus* and has the 2nd lateral tooth fused/appressed to the 1st lateral tooth; in *D. fusconotatus* the 6th lateral tooth is fused/appressed to the 5th, and the 1st and 2nd lateral teeth are separate. Larvae also differ in size, *D. fusconotatus* being much larger, and in ventromental strial ridge counts (20–22 in *fusconotatus,* 27–29 in *septemmaculatus,* 22–26 in *sudanicus*). The pupal and larval data are based on a very small sample.

PUPA: (n = 5)

COLOR. Light yellow-brown, with light brown along lateral margins of tergites.

LENGTH. Total 3.21 mm (1). Cephalothorax 0.83 mm (1). Abdomen 2.38–3.10, 2.77 mm (3).

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 12J), 45–47 (2) high, 65–88 (2) wide. Dorsum moderately pebbled. Dc_2 closer to Dc_1. Thoracic horn base (Fig. 12K) with tracheal bundles separate.

ABDOMEN. Similar to *D. fusconotatus* (Fig. 10C). Sternite I with very fine median shagreen spinules; sternites II-III with fine lateral shagreen bands; also fine spinules scattered over S II-III; Tergite I with anteromedian weak reticulate pattern; T II with median quadrilateral shagreen area; T III-V with larger median quadrilateral shagreen area, areas somewhat extended laterally on anterior and/or posterior portion; T VI with broadly V shaped shagreen area; T VII with an anterior pair of suboval shagreen areas; T VIII with a pair of longitudinal bands of fine shagreen, or an anterior and posterior ovoid to reniform pair of fine shagreen areas; shagreen areas on T II-VI with spines larger in middle and posterior portion of area. Well developed shagreen area present dorsally on anal lobe. Tergites III-V with posterior conjunctival band of fine spinules; T VI-VIII with reticulate cuticular pattern posterolaterally well developed on T VI-VII. Posterior margin of T II with transverse row of 56–70, 63 hooklets. T VIII with 5 lateral setae. Caudolateral spurs on T VIII single or multiple, small (similar to *D. fusconotatus,* Figs. 10D, E). Anal lobes with 35–47, 40 setae. DR 2.50–2.69, 2.57.

FOURTH INSTAR LARVA: (n = 5)

COLOR. Head capsule light brown, mentum and postocciput red-brown; postmentum not darkened.

HEAD. Postmentum length 175–193, 182. Mandible length 163–165, 164 (3) with three lateral teeth; 2 dorsal teeth present. Pecten mandibularis composed of 8–10, 9 (4) setae. Mentum (Fig. 12L) with 13 teeth, 1st and 2nd teeth fused or closely appressed; width 100–110, 105 (4); MR 2.38–2.64, 2.51 (3). Ventromental plate with mostly smooth anterior margin, sometimes with extremely shallow crenulations; width 81–87, 83 (4); length 40–43, 41 (4). VPR 1.91–2.18, 2.03 (4); IPD 46–51, 49 (4); PSR 1.61–1.89, 1.69 (4); 22–26, 24 strial ridges. Length of antennal segments: 52–61, 57 (4); 14–16, 15 (4); 8–9, 9 (3); 13 (2); 6 (3). AR 1.21–1.39 (2) (Fig. 12M). Inner blade of premandible greater than outer blade. Pecten epipharyngis with 4–5, 5 lobes. Anterior margin of frontal apotome with long, thin ventral frontal process; labral sclerite 1 smooth. S I with 5–7, 6 fringes.

BODY. Ventral tubuli absent.

MATERIAL EXAMINED: MALAGASY: Pr. Tanan, Antanifotsy R. (20° C), at forest station, 31-X-71, G.F. & C.H. Edmunds, F. Emmanuel, 1 male (FS). NIGERIA: Kaduna, 19-X-1956, B. McMillan, 2 males (BM); Lake Opi nr Nsukka, light trap, 26-26-XI-1978, leg L. Hare, 1 female (CH). SUDAN: Adok, 21-XI-1953, 1 male (holotype) (BM); Leidnum nr Wau, III-IV-1955, E.T.M. Reid, 1 male (paratype) (BM); Melut, 17-XI-1953, E.T.M. Reid, 1 female (paratype) (BM). TANZANIA: U. Pangani Rv, Ngumba Ya Mungu Reservoir, emergence trap, 15-VIII-1973, R.G. Bailey, 1 male (BM). [ZIMBABWE?]: Lake Karibe, 1966, leg. A.J. McLachlan, 1 male, 6 Pex, 6 Lex (BM).

FIG. 8. Superior volsellae of some Afrotropical *Dicrotendipes*. A, B) *D. freemani*. C, D) *D. chambiensis*.

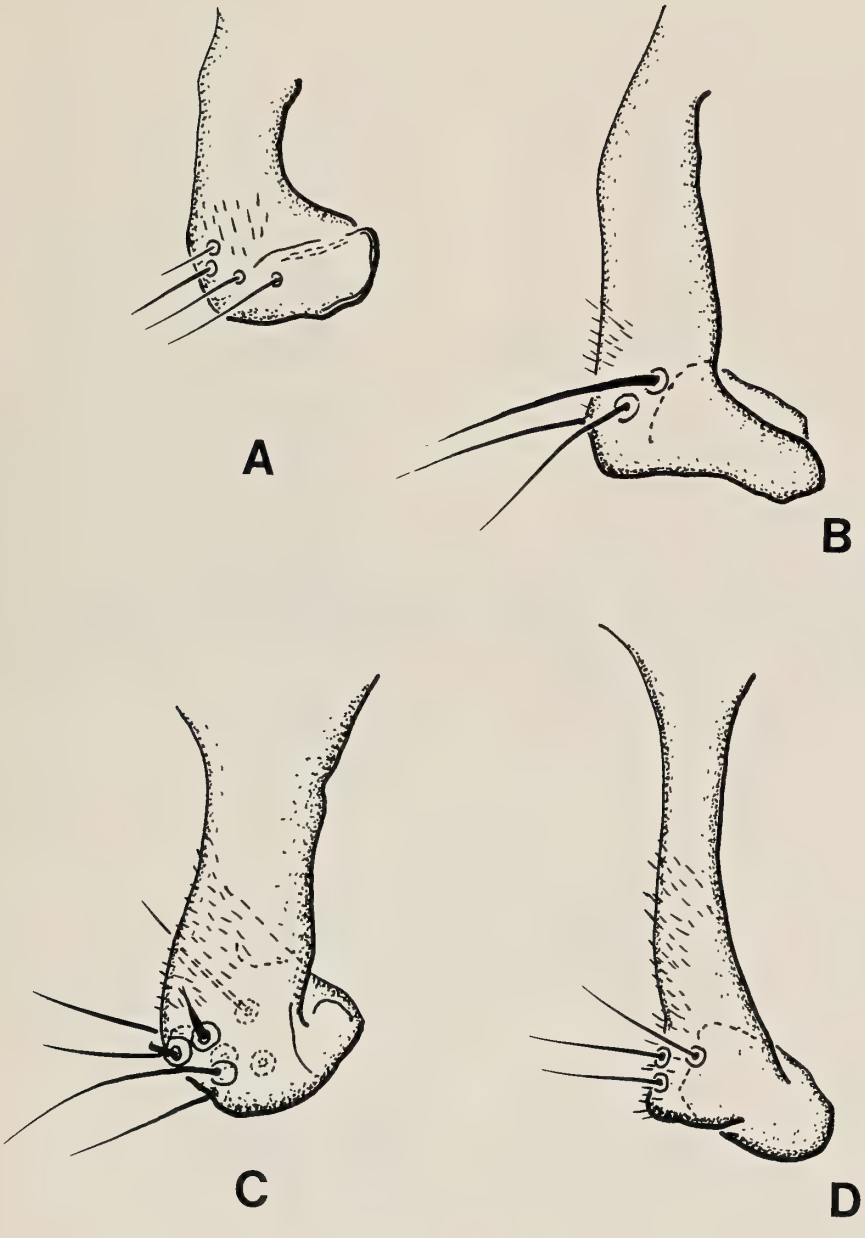
A
B
C
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FIG. 9. *D. cordatus,* pupa. A) cephalic tubercles. B) Thoracic horn bases from 2 specimens. C) Abdomen, dorsal. D, E) Caudolateral spurs on T VIII.

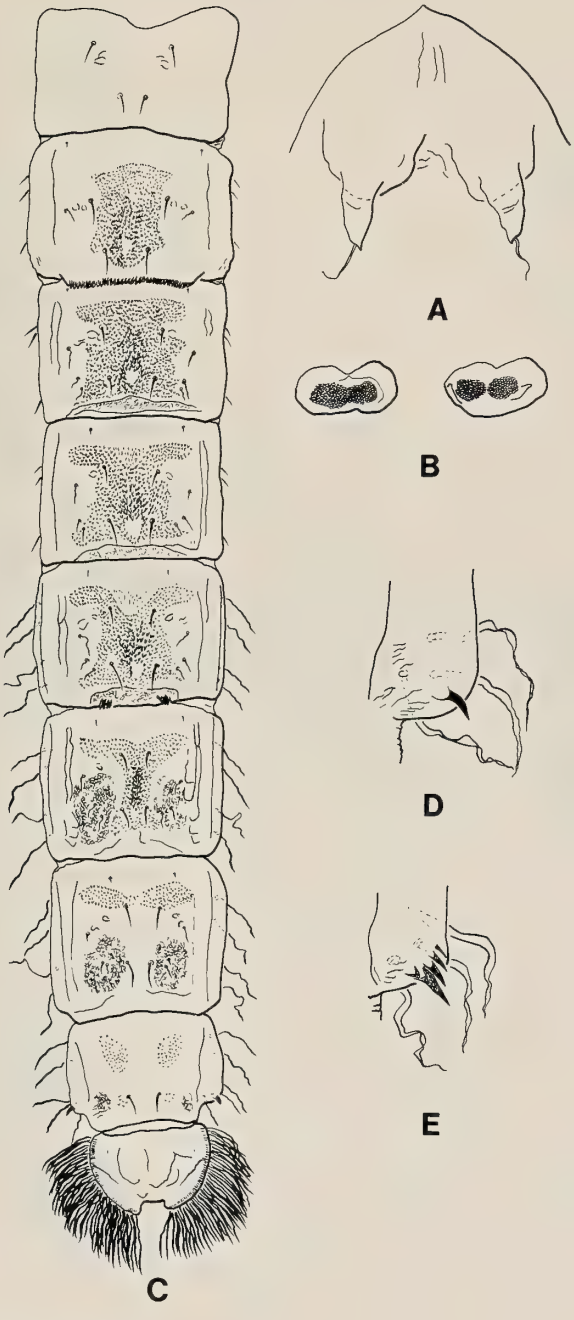
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FIG. 10. *D. fusconotatus,* pupa (A–E) and larva (F–L). A) Cephalic tubercle. B) Thoracic horn base. C) Abdomen, dorsal. D, E) Caudolateral spurs on T VIII. F) Mandible, ventral. G) Mandible, dorsal. H) Mentum and ventromental plate. I) Antenna. J) Premandible. K) Pecten epipharyngis. L) S I.

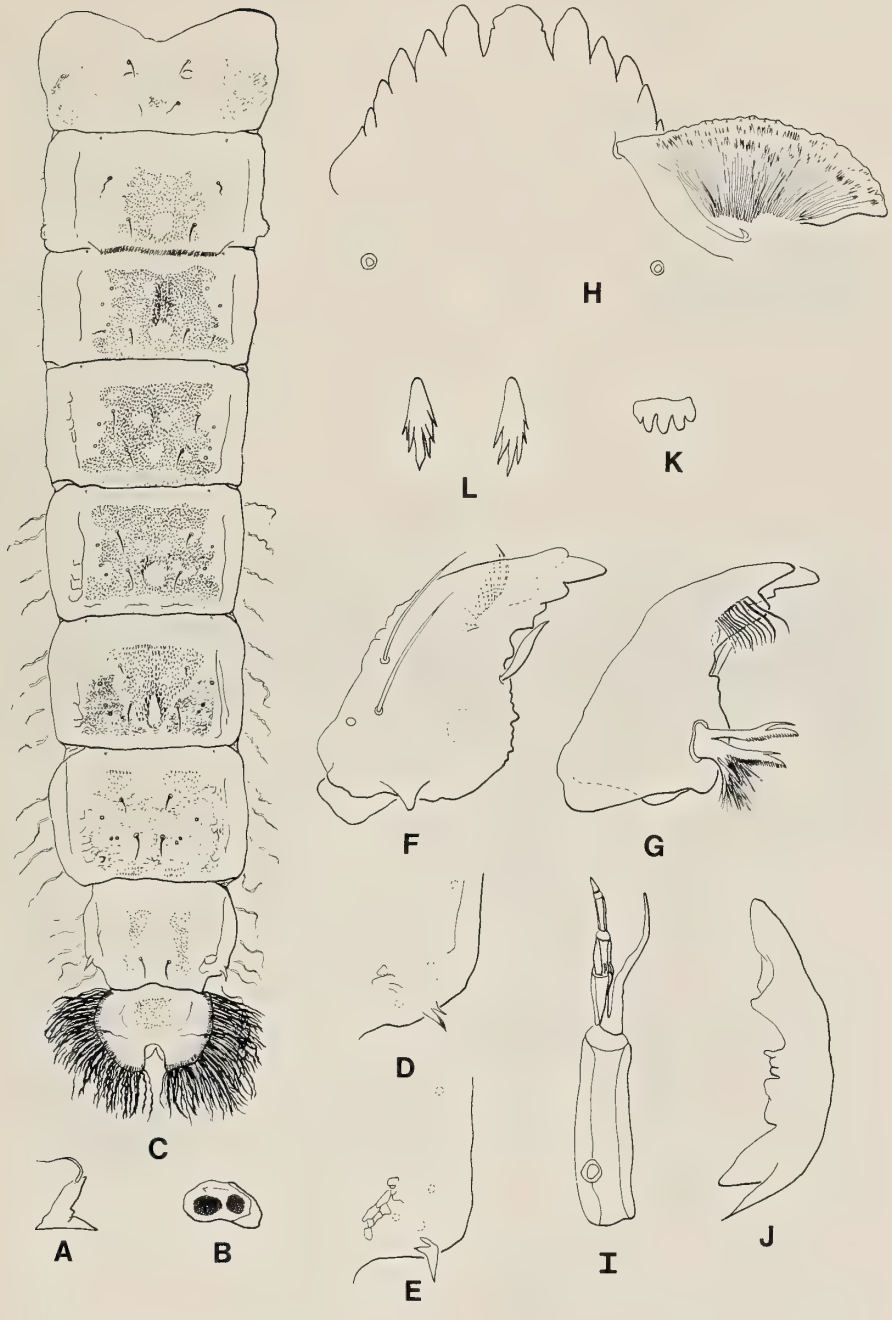
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FIG. 11. *D. kribiicola,* pupa (A–D) and larva (E–J). A) Cephalic tubercle. B) Thoracic horn base. C) Abdomen, dorsal. D) Caudolateral spur on T VIII. E) Mandible, ventral. F) Mentum and ventromental plate. G) Antenna. H) Premandible. I) Pecten epipharyngis. J) Frontal apotome and labral sclerites. K) S I.

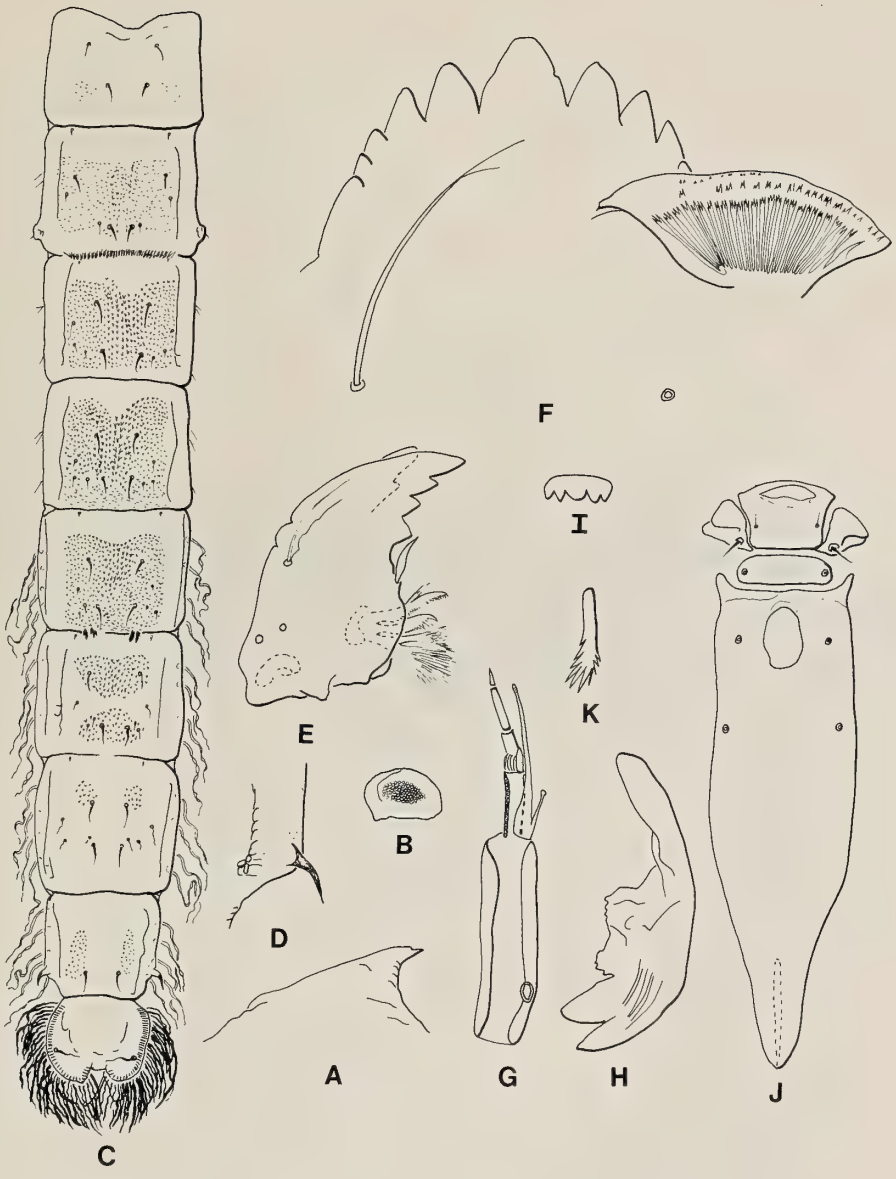
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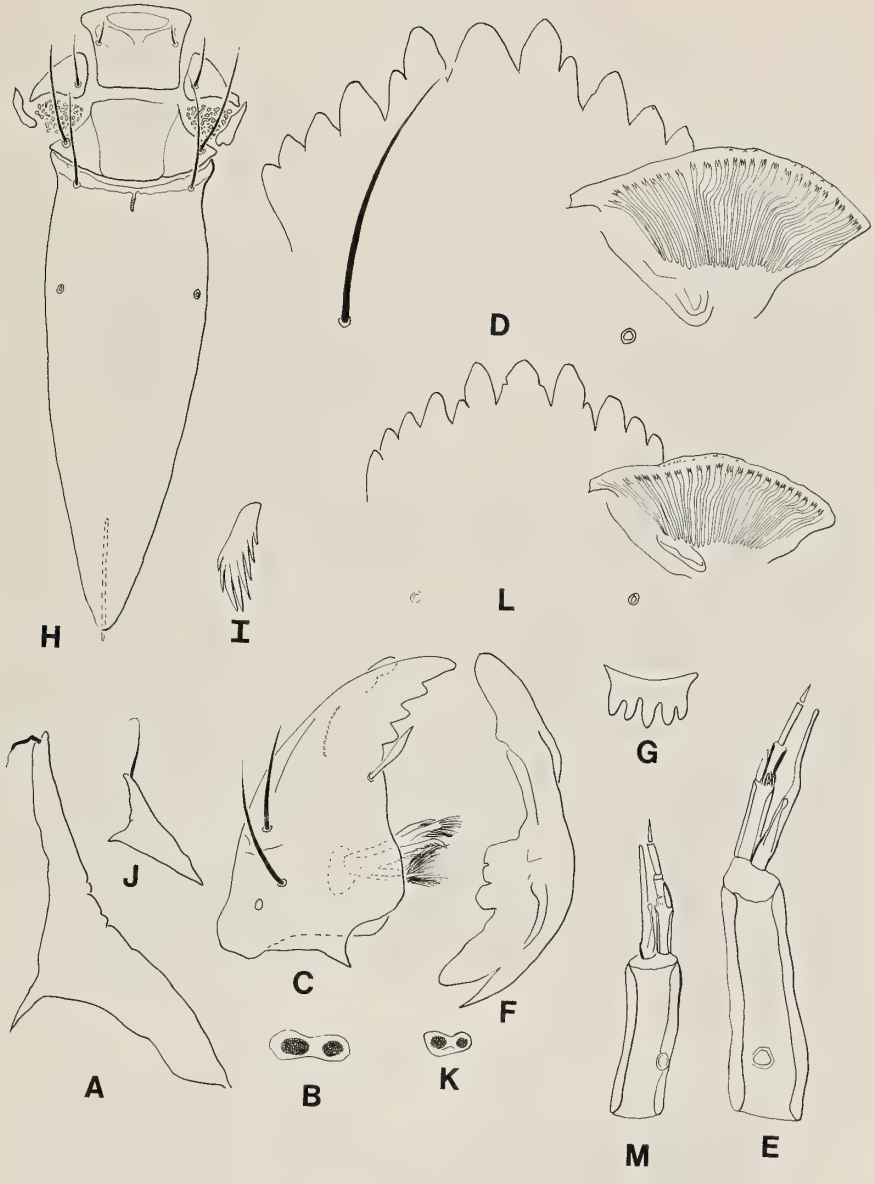
FIG. 12. *D. septemmaculatus,* pupa (A, B) and larva (C–I). A) Cephalic tubercle. B) Thoracic horn base. C) Mandible, ventral. D) Mentum and ventromental plate. E) Antenna. F) Premandible. G) Pecten epipharyngis. H) Frontal apotome and labral sclerites. I) S I. *D. sudanicus,* pupa (J, K) and larva (L, M). J) Cephalic tubercle. K) Thoracic horn base. L) Mentum and ventromental plate. M) Antenna.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Chapter III.
The Neotropical *Dicrotendipes*

With only a few exceptions (Brundin 1966; Edwards 1931; Reiss 1972, 1974), the Chironomidae of South America have not been studied in great detail. Reiss (1977a, 1982) has summarized the majority of papers dealing with the taxonomy of the family from South America.

The *Dicrotendipes* of the Neotropical region are poorly known. Rempel (1939:213) described a species from Brazil, *Chironomus* (*Calochironomus*) *atripennis,* which may be a *Dicrotendipes.* However, I have not seen any material of this species, and the description and figures are not sufficient to place this species in *Dicrotendipes.* Fittkau & Reiss (1979) listed one described and 10 undescribed species of *Dicrotendipes* from tropical and subtropical South America. To date, only 6 species have been described from the region (Paggi 1975, 1978, 1987; Epler 1987b). In this chapter, I review the known species, and supply descriptions for 10 new species, 9 of which are from the Amazon area.

It is unfortunate that the immature stages, especially the larvae, remain unknown for the majority of the species described here. As a result, the majority of the Neotropical species could not be used in the phylogenetic analysis (Chap. VI).

Many of the species from the Amazon area are quite bizarre, e.g., *D. soccus,* when compared with the Holarctic or Afrotropical fauna. All species from South America with deeply bifid inferior volsellae known to me possess palmate sensilla chaetica on the hind metatarsus. Such sensilla chaetica are lacking in Afrotropical forms with deeply bifid inferior volsellae (but are present in 2 species with simple inferior volsellae from the Oriental-Australasian region, and in one species from the Neotropics, *D. alsinensis*).

I have little doubt that more species of South American *Dicrotendipes* remain to be discovered and described. The following key must be considered as incomplete in this respect. Because the immature stages of Neotropical *Dicrotendipes* remain largely unknown, no keys are offered for their identification. Paggi (1987) offered a key for all stages of Argentinian *Dicrotendipes* known to her.

Key to Adult Males of Neotropical *Dicrotendipes*

1. Inferior volsella simple or at most deeply notched apically (Figs. 13-16); palmate sensilla chaetica absent on male hind metatarsus (except in *D. alsinensis;* see couplet 5) . 2
   Inferior volsella deeply bifid, each lobe well separated (Figs. 17, 19, 20, 24-27) or inferior volsella stout and extremely setose (Figs. 18, 23); palmate sensilla chaetica present on male hind metatarsus 7

2. Base of anal point raised, truncate, with more than 10 dorsal basal setae (Fig. 16) . . . . . *D. sinoposus* Epler
   Base of anal point not truncate; 7 or fewer dorsal basal setae 3
3. Superior volsella with short ventral, basal membranous flap (Fig. 22) . . . . . *D. palearivillosus* sp. nov.
   Superior volsella without membranous flap 4
4. Superior volsella cylindrical-digitiform with membranous apex 5
   Superior volsella pediform 6
5. Foretarsal beard well developed; gonostylus moderately heavy; superior volsella stout (Paggi 1975: Figs. 5, 8); with palmate sensilla chaetica on hind metatarsus . . . . . *D. alsinensis* (Paggi)
   Foretarsal beard absent; gonostylus thin; superior volsella thin (Fig. 13); without palmate sensilla chaetica on hind metatarsus . . . . . *D. aethiops* (Townes)
6. Superior volsella with elongate thin basal portion, "foot" narrow; inferior volsella deeply notched apically, lobes almost completely separated (Paggi 1978: Figs. 3, 5) . . . . *D. nestori* Paggi
   Superior volsella with thicker basal portion, "foot" robust; inferior volsella shallowly notched or simple (Figs. 13-16) 7
7. Mid leg metatarsus very short, $SV_2 > 5.00$; inferior volsella simple; wings mostly clear (Paggi 1987: Figs. 2a, 6a) . . . . . *D. pellegriniensis* Paggi
   Metatarsus normal, $SV_2 < 5.00$; inferior volsella simple or slightly notched apically (Figs. 14-15); wings with faint markings at base of r_{4+5}, at FCu and along M_{3+4} and Cu_1 8
8. General coloration yellow-brown to brown; legs stramineous-brown, fore femora with darkened apices . . . . . *D. californicus* (Johannsen) complex (*D. californicus, D. crypticus* Epler, *D. embalsensis* Paggi
   General coloration red-brown; legs dark brown, fore femora solid dark brown . . . . *D. obrienorum* Epler
9. Inferior volsella stout, covered with long, dense setae 10
   Inferior volsella thin to moderate, without long, dense setae 11
10. Ventral portion of bifid superior volsella with sensilla chaetica (Fig. 18) (ventral portion of volsella is often difficult to discern) . . . . . *D. dasylabidus* sp. nov.
    Ventral portion of bifid superior volsella without sensilla chaetica (Fig. 23) (ventral portion of volsella is often difficult to discern) . . . . *D. paradasylabidus* sp. nov.
11. Base of anal point with ventral bulbous swelling (Figs. 17, 20, 24, 25) 14
    Base of anal point without ventral bulbous swelling (Figs. 19, 26, 27) 12
12. Disto-ventral portion of distal arm of inferior volsella with long sensilla chaetica; superior volsella slipper-shaped; posterior margin of T IX strongly cordiform-emarginate at base of anal point (Fig. 27) . . . . . *D. soccus* sp. nov.
    Not as above 13
13. Superior volsella deltoid-pediform in dorsal view (Fig. 26) . . . . . *D. reissi* sp. nov.
    Superior volsella elongate-cylindrical with pointed apex and dorsal basal lobe from which volsella is suspended (Fig. 19) . . . . . *D. demissus* sp. nov.
14. Superior volsella bifid (Fig. 25) . . . . . *D. radinovskyi* sp. nov.
    Superior volsella not bifid 15
15. Superior volsella with acute apex directed caudad (Fig. 17) . . *D. amazonicus* sp. nov.
    Superior volsella deltoid-pediform or pediform (Figs. 21, 24) 16
16. Superior volsella pediform, apex directed laterad (Fig. 24) . . . *D. paterjohni* sp. nov.

Superior volsella deltoid-pediform, apex membranous and ventrally produced (may be directed mediad or laterad) (Fig. 20) . . . . . *D. fittkaui* sp. nov.

Previously Described Species

Dicrotendipes aethiops (Townes) (Figs. 13, 48)

Tendipes (*Limnochironomus*) *aethiops* Townes, 1945:107.
Tendipes (*Limnochironomus*) *figueroai* Vargas, 1952:48.
Dicrotendipes aethiops (Townes): Epler 1987a:30.

See Epler (1987a) for complete synonymy and description of adult male, and Epler (1987b) for additional distribution records. This species occurs in the southwestern United States and Mexico, and may occur farther south.

Dicrotendipes alsinensis (Paggi)

Chironomus (*Dicrotendipes*) *alsinensis* Paggi, 1975:149.
Dicrotendipes alsinensis (Paggi): Paggi 1978:235.

See Paggi (1975:149) for description of adult male, pupa and larva. To Paggi's (1975) description I can add the following data: Adult male: 12 cibarial setae; mid leg metatarsus with 10 palmate sensilla chaetica, hind metatarsus with 3 palmate sensilla chaetica; wing setae: R 18, R_1 7, R_{4+5} 4; no ventral accessory setae on S VI. Larva: 23 ventromental plate strial ridges, anterior margin of ventromental plate crenulated.

On the basis of superior volsella morphology (digitiform-cylindrical with a membranous apex), *D. alsinensis* would appear to be a member of the *D. nervosus* group as defined by Epler (1987a). However, Paggi's (1975:Fig. 12) pupal illustration does not indicate that the median shagreen area on T VI is V-shaped and the one pupal specimen I examined is damaged; T VI is not observable. Because the frontal apotome and labral sclerite 1 are not clearly visible on the larval exuviae associated with this pupal specimen (and they are not described by Paggi 1975), this species is difficult to place. It may be related to the *modestus* group, the *nervosus* group or *D. fumidus*. However, the one male of this species that I examined possesses palmate sensilla chaetica on the hind metatarsus; these sensilla chaetica are not present on any of the members of the aforementioned groups.

MATERIAL EXAMINED: ARGENTINA: Prov. Buenas Aires, Laguna Alsina, 27-III-1975, 1 male (IL); same locality, 27-IV-1975, leg. Paggi, 1 pharate male pupa/Lex (IL).

Dicrotendipes californicus (Johannsen) (Figs. 14, 47)

Chironomus californicus Johannsen, 1905:217.

See Epler (1987a) for full synonymies and descriptions of adult male, pupa and larva.

This species is widespread from California, southern Idaho and South Dakota in the U.S. south to Chile. Four other apparently closely related species have been described: *D. crypticus* Epler from New Mexico and California (Epler 1987a), *D. obrienorum* Epler from Mexico (Epler 1987b), and *D. embalsensis* Paggi and *D. pellegriniensis* Paggi from Argentina (Paggi 1987). These 4 species may only represent variants or ecotypes of *D. californicus*. More data are needed to clarify their status. See also discussions under each species below.

I have examined a single male specimen from the NM (collected at Finca Richter nr Bogotá, Colombia, by Lichtenberg) which may represent a new species. However, it is quite possible that this specimen is a *D. californicus* (or *D. obrienorum*) with deformed superior volsellae. I would have to see more specimens of this type before I could justify describing it as a new species.

There is minor variation in wing maculation over this species' range. A specimen from Peru has wing markings which are similar, but darker and more pronounced, than the typical *D. californicus*. See also comments under *D. pellegriniensis* below.

In addition to the material listed below, material from Costa Rica and Mexico has been examined (Epler 1987a).

MATERIAL EXAMINED: CHILE: Coquimbo, Punta Teatinos, 16-IX-1952, leg. P.G. Kuschel, 1 male (US); Santa Maria Fuadu [?], 28-I-1943, E. Melland, 1 male (BM). COLOMBIA: Palmira, Lichtfang [light trap], 25-I-1975, leg. Lichtenberg, 1 male (NM); Palmira, Finca Austria, b. Schwimmbecken, 26-I-1975, leg. Lichtenberg, 1 male (NM). PANAMÁ: Chiriquí Prov., Presa Fortuna, holding pond above Aoki camp, 3900′, light trap, 25-V-1985, leg. R.W. Flowers, 1 male (JE). PERU: Laguna de Medio Mundo, vegetation, brackish water of northern Peruvian coast, 17-IV-1975, leg. Gloria S. Minaya Gómez, 1 male, 1 larva (ZS).

Dicrotendipes crypticus Epler? (Fig. 47)

Dicrotendipes crypticus Epler, 1987a:39.

I have seen one larval specimen from South America which fits my concept of this species. The specimen possesses a head capsule with grainy integument, 27 ventromental plate strial ridges and a crenulate anterior margin

on the ventromental plate. This specimen may belong with *D. embalsensis*. The larvae of these 2 species appear identical, and the 2 species may prove to be synonyms. The date of publication of both Epler 1987a and Paggi 1987 is March 1987. Although *D. crypticus* was originally described in my thesis (Epler 1983), theses are not considered publications by the International Code of Zoological Nomenclature, Article 9 (1985). However, until more specimens of both species are examined, no decision can be made concerning their status.

MATERIAL EXAMINED: PARAGUAY: Rio Pilcomayo, 31-III-1974, leg. H. Sioli, 1 larva (ZS).

Dicrotendipes embalsensis Paggi

Dicrotendipes embalsensis Paggi, 1987:703.

See Paggi (1987:703) for description of adult male, pupa and larva. To her description I can add the following data: Adult male: 8 cibarial setae; mid leg metatarsus with 13–14 palmate sensilla chaetica, 0 on hind metatarsus; wing setae; squama 18–21, R 18, R_1 4, R_{4+5} 12; no ventral accessory setae apparent on S VI. Larva: 29–30 ventromental plate strial ridges, anterior margin of plate weakly and shallowly crenulated.

The key character of adult male frontal tubercle length used by Paggi (1987:697) will probably not separate *D. embalsensis* from *D. pellegriniensis*. The one specimen of *D. embalsensis* I examined lacked frontal tubercles. The length and presence or absence of frontal tubercles is extremely variable in all species of *Dicrotendipes* I have examined when sufficient material (usually more than 10 specimens) was available. The same would probably hold true for squamal setal counts (the one specimen I examined had a lower squamal setal count, 18, than recorded in the description or used in the keys). As adults, the 2 species can be separated by the short metatarsus and apparently clear wings of *D. pellegriniensis*. The characters used to separate the larvae of these 2 species in Paggi (1987) will probably also fail to separate them when more material is examined. Postmental darkening may be environmentally influenced (it apparently is in many Nearctic species; see Epler 1987a); and there probably is not a significant difference between a pecten epipharyngis with 5 teeth (*D. embalsensis*) and one with 6–7 teeth (*D. pellegriniensis*). More specimens of all species of the *D. californicus* complex must be examined in order to determine which characters, if any, will separate the species. It is possible that all of these species are nothing more than variants or ecophenotypes of *D. californicus*.

MATERIAL EXAMINED: ARGENTINA: Prov. Neuquén, Lago Ramos Mexia, 4-X-1983, leg. Kaisin, 1 male/Pex/Lex (IL).

Dicrotendipes nervosus (Staeger) group (Fig. 45)

I have seen several larval specimens from Brazil which conform to my definition of the *D. nervosus* group (cf. Epler 1987a). All of these specimens possess a pair of ventral tubuli on the eighth abdominal segment. It is possible that these larvae may belong with one or several of the species described as new below. Pupae are known for only 2 of these species, *D. fittkauii* and *D. soccus*. None of the pupal specimens examined possessed ventral tubule remnants on S VIII; these remnants should have been present had the larvae possessed ventral tubules. The pupae of both of these species possess a V-shaped median shagreen area on T VI, which would place them in the *D. nervosus* group. However, without associated larvae, such placement must be considered uncertain.

MATERIAL EXAMINED: BRAZIL: Amazonas: Lago do Calado, lower Rio Solimões, nr village Manacapurú, experimental box filled with wood wool as artificial substrate, exposed free floating at border of marginal floating meadows, Autumn 1968, leg. W. Junk, 1 larva (ZS). Pará: Lago Salgado, Cabaciera do boi, zw. Tabacorana-Wurzeln, 13-IV-1948, leg. Braun, 1 larva (ZS); same locality & collector, Aufwuchs auf Canaranca, 16-IV-1948, 1 larva (ZS).

Dicrotendipes nestori Paggi

Dicrotendipes nestori Paggi, 1978:235.

See Paggi (1978:235) for description of adult male, pupa and larva. To her description I can add the followng data: Adult male: 9 cibarial setae; mid leg metatarsus with 7 palmate sensilla chaetica, 0 on hind metatarsus; wing setae: R 19, R_1 7, R_{4+5} 12; no ventral accessory setae apparent on S VI.

I have not examined any larvae or pupae of this species. Because Paggi (1978) did not describe the immature stages completely, this species can not be placed phylogenetically.

MATERIAL EXAMINED: ARGENTINA: Prov. Buenas Aires, Laguna Alsina, 27-III-1975, 1 male (paratype) (IL).

Dicrotendipes obrienorum Epler (Figs. 15, 47)

Dicrotendipes obrienorum Epler, 1987b.

See description in Epler (1987b). Known only from Mexico, this species may be a lower latitude but higher elevation variant of *D. californicus.*

Dicrotendipes pellegriniensis Paggi

Dicrotendipes pellegriniensis Paggi, 1987:695.

See Paggi (1987:695) for description of adult male, pupa and larva. To her description I can add the following data: 10 cibarial setae; at least 14 palmate sensilla chaetica on mid leg metatarsus (not clearly discernible), 0 palmate sensilla chaetica on hind metatarsus; wing setae: R 16, R_1 6, R_{4+5} 9; no ventral accessory setae apparent on S VI. Larva: ventromental plate with 34 strial ridges, anterior margin of plate smooth.

The larvae and pupae of this species are morphologically inseparable from *D. californicus.* The adult male differs from *D. californicus* in the very short mid leg metatarsus which results in a very high SV_2 (6.46 in the one specimen made available to me), and perhaps in wing maculation. Paggi (1987) described the wings of this species as transparent, without spots. Unfortunately, in the one specimen of this species available to me, the mountant under the cover slip over the wings is unclear and the wings can not be viewed clearly. However, there appears to be a spot in the apex of cell r_{4+5}. I have found the amount or intensity of wing maculation to be variable in Nearctic specimens of *D. californicus;* thus, this character may not be of use in species separation within the *D. californicus* complex. The inferior volsella of *D. pellegriniensis* differs from that of typical *D. californicus* in that there is no trace of an apical indentation. This character is unreliable, however, for in many species the amount of apical indentation of the inferior volsella is variable. It is quite possible that *D. pellegriniensis* is but an ecophenotype of *D. californicus.* Paggi (1987) does not supply any physicochemical data for the collection sites of this species; perhaps an unknown pollutant could cause morphological changes which may produce a population of aberrant individuals, which may then be described as a "new species." More research is needed to solve the complexities of this problem.

MATERIAL EXAMINED: ARGENTINA: Prov. Rio Negro, Lago Pellegrini, 25, 26-III-1979, leg. Paggi, 1 male, 1 pupa/Lex (IL).

Dicrotendipes sinoposus Epler (Figs. 16, 48)

Dicrotendipes sinoposus Epler, 1987b.

See description in Epler (1987b). Originally described from Mexico, I have since examined more material from the Neotropics. These additional specimens enable me to add the following data to the original description: AR 2.22–2.70; 7–9 palmate sensilla chaetica on metatarsus of middle leg; 0–4 ventral accessory setae on S VI.

MATERIAL EXAMINED: BRAZIL: [Pará]: Rio Tocantins, nr village Jatobal, light trap, 5-XI-1960, leg. E.J. Fittkau, 1 male (ZS); Amazonas: Lago Cabaliana, lower Rio Solimões, drift, 16-VI-1971, leg. F. Reiss, 1 male (ZS). COLOMBIA: Arbeláez, light trap, 26-XI-1974, leg. Lichtenberg, 1 male; same locality & collector, 30-XI-1974, 1 male (NM). DOMINICA: Pont Casse, 1.5 mi. N, rain forest, 12 Feb 1965, leg. W.W. Wirth, Bredin-Archbold-Smithsonian Biol. Survey Dominica, 2 males (US).

New Species Descriptions

Dicrotendipes amazonicus sp. nov. (Fig. 17)

TYPE LOCALITY: Rio Tupani, lower Rio Madeira, Amazonas, Brazil.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas: Rio Tupani, lower Rio Madeira, light trap, 14-15-IX-1960, leg. E.J. Fittkau (ZS). **Paratypes** (2572): same data as holotype, 2553 males, 13 females (ZS); lower Rio Madeira, Paraná Madeirinha, light trap, 12-IX-1960, leg. E.J. Fittkau, 4 males (ZS); Rio Tupani (wide, lake-like), light trap, 21-IX-1960, leg. E.J. Fittkau, 3 males (ZS); Upper Rio Tapajós, slightly downstream from mouth of Rio Juruena & Rio São Manuel, light trap at village Barra, 13-I-1961, leg. E.J. Fittkau, 1 male (ZS). Holotype to be deposited in IN; paratypes in ZS, JE.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella, distinctive superior volsella and bulbous swelling beneath the anal point will distinguish this species.

ETYMOLOGY. This species is named for the Amazon region.

MALE IMAGO (n = 6)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with light brown veins.

LENGTH. Total 3.20–3.65, 3.33 mm. Thorax 0.72–0.82, 0.78 mm. Abdomen 2.43–2.85, 2.56 mm.

HEAD. Setae: temporal 22–32, 27; clypeal 10–14, 12; cibarial 7–8, 8 (4). Palpomere lengths: 27–40, 35; 35–40, 38; 70–88, 79; 106–113, 111; 148–180, 170 (4). Frontal tubercles 7–20, 12 long, 6–7, 7 wide (5). AR 2.03–2.15, 2.09 (3).

THORAX. Scutal tubercle well developed; humeral pit with 5–7 small tubercles. Acrostichals 6–9, 7; dorsocentrals 13–17, 15 (5); scutellars 7–8, 7; prealars 6–8, 7 (5).

WING. Length 1.28–1.40, 1.36 mm (5); width 0.39–0.41, 0.40 mm (5). FCu distal to RM. VR 0.85–0.88, 0.86 (5). Setae: brachiolum 2; squama 1–2, 2; R 12–16, 14; R_1 5–8, 7; R_{4+5} 9–14, 12.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 5–9, 7 on middle metatarsus, 2–4, 3 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	745-850, 789	620-700, 655	680-790, 727
ti	455-530, 486	540-610, 577	700-800 743
ta_1	1050-1170, 1109 (5)	310-365, 338	460-530, 497
ta_2	490-550, 519 (5)	140-170, 160	225-265, 247
ta_3	420-490, 456 (5)	100-120, 112	180-210, 197
ta_4	305-420, 388 (5)	45-50, 49 (5)	90-105, 98
ta_5	150-175, 168 (5)	50-55, 51 (5)	65-80, 76 (5)
LR	2.19-2.35, 2.26 (5)	0.57-0.61, 0.59	0.66-0.69, 0.67
BV	1.51-1.62, 1.57 (5)	4.09-4.41, 4.26 (5)	3.14-3.29, 3.19 (5)
SV	1.14-1.18, 1.16 (5)	3.55-3.76, 3.64	2.88-3.00, 2.96

ABDOMEN. 1–4 ventral accessory setae on S VI; 1 specimen seen with 1 ventral accessory seta on S V.

HYPOPYGIUM (Figs. 17A, B) with 2–5, 4 medial setae. Gonostylus normal, curved medially, with 4–7, 6 preapical setae. Superior volsella (Figs. 17C, D) length 50–72, 61 (4); width 27–30, 29 (4); LWR 1.9–2.6, 2.2 (4); slipper-shaped in dorsal view; with 4–5, 5 sensilla chaetica and fine setae on medial surface. Inferior volsella length 105–130, 117 (4); deeply bifid, with 3–5 sensilla chaetica in single row on proximal lobe, 4–5 sensilla chaetica in single row on distal lobe; distal lobe with 1 well developed ventral preapical seta. Anal point bare dorsally, with basal peduncle and bulbous ventral extension, weakly deflexed; with 1–2 dorsal basal setae and 6–13, 10 lateral basal setae.

FEMALE IMAGO (n = 3)

COLOR (slide mounted specimens). Similar to male.

LENGTH. Total 2.23–3.04, 2.56 mm. Thorax 0.74–0.81, 0.78 mm. Abdomen 1.42–2.30, 1.77 mm.

HEAD. Setae: temporal 22–23, 23; clypeal 11–14, 12; cibarial 7–10, 9. Palpomere lengths: 30–35, 33; 40–42, 41; 80–85, 83; 112–115, 115; 165–175, 170. Frontal tubercles 9–18, 12 long, 5–10, 7 wide. AR 0.47–0.55, 0.50.

THORAX. Scutal tubercle well developed; humeral pit with about 4 small tubercles. Acrostichals 9–10 (2); dorsocentrals 22–29, 25; scutellars 7–9, 7; prealars 6–8, 7.

WING. Length 1.49–1.55, 1.53 mm; width 0.47–0.51, 0.50 mm. FCu distal to RM. VR 0.82–0.89, 0.87. Setae: brachiolum 2; squama 1–4, 2; R 16–18, 17; R_1 11–16, 13; R_{4+5} 27–32, 29.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 15–20, 17 on middle metatarsus, 5–7, 6 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	790-800, 793	660-695, 675	745-790, 762
ti	500-520, 510	595-620, 606	745-790, 778
ta_1	1125-1240 (2)	355-370, 362	470-520, 493
ta_2	530-570 (2)	150-160, 157	225-250, 233
ta_3	450-510 (2)	105-110 107	180-195, 188
ta_4	430-560 (2)	45-50, 48	90
ta_5	190 (2)	50	70-75, 72
LR	2.25-2.43 (2)	0.60	0.62-0.65, 0.63
BV	1.47-1.51 (2)	4.44-4.64, 4.54	3.43-3.58, 3.49
SV	1.05-1.15 (2)	3.51-3.56, 3.54	3.06-3.19, 3.12

ABDOMEN. 2–4 ventral accessory setae on S VI. Notum 148–157, 153; cerci 72–90, 82. S VIII with 11–15 setae/side; X with 4–6, 5 setae; Gc IX with 1–2, 2 setae/side. DmL, VIL and ApL as in Fig. 17E.

Dicrotendipes dasylabidus sp. nov. (Fig. 18)

TYPE LOCALITY: Brazil. Amazonas, Upper Rio Solimões, Florianopolis.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas: Upper Rio Solimões, Florianopolis, light trap, 15-VIII-1961, leg. E.J. Fittkau (ZS). Holotype to be deposited in IN.

DIAGNOSIS: The immaculate wings, stout, deeply bifid and densely setose inferior volsella, distinctive bifid superior volsella and cordiform-emarginate base of the anal point will distinguish this species.

ETYMOLOGY. From the Greek *dasys,* hairy and *labidos,* forceps; refers to the densely setose inferior volsella.

MALE IMAGO (n = 1)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with light brown veins.

LENGTH. Total 3.64 mm. Thorax 0.91 mm. Abdomen 2.73 mm.

HEAD. Setae: temporal 33; clypeal 11; cibarial 9. Palpomere lengths: 41, 47; 93; 115; 190. Frontal tubercles 6 long, 6 wide. AR 2.08.

THORAX. Scutal tubercle well developed; humeral pit indiscernible. Acrostichals 9; dorsocentrals 14; scutellars 10; prealars 8.

WING. Length 1.58 mm; width 0.47 mm. FCu distal to RM. VR 0.83. Setae: brachiolum 2; squama 2; R 15; R_1 6; R_{4+5} 11.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 8 on middle metatarsus, 5 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	855	710	830
ti	550	655	860
ta_1	1130	390	550
ta_2	530	190	280
ta_3	450	135	220
ta_4	400	50	100
ta_5	190	55	70
LR	2.05	0.60	0.64
BV	1.61	4.08	3.34
SV	1.24	3.50	3.07

ABDOMEN. Ventral accessory setae on S VI not apparent.

HYPOPYGIUM (Fig. 18A) with 4 medial setae. Gonostylus normal, curved medially, with 4 preapical setae. Superior volsella (Fig. 18B) bifid; length of dorsal portion 54, ventral portion 90; width of dorsal portion 11, ventral portion 30; dorsal portion small, digitiform, sclerotized, with 2 sensilla chaetica; ventral portion thin, lamellar, densely setose, with 2–4 sensilla chaetica. Inferior volsella length 135; deeply bifid, stout, with 4 sensilla chaetica each on proximal and distal lobes, densely setose on inner margin, with 1 well developed ventral preapical seta. Anal point cordiform-emarginate basally, bare dorsally; with 14 dorsal basal setae and 9 lateral basal setae.

Dicrotendipes demissus sp. nov. (Fig. 19)

TYPE LOCALITY: Brazil, Amazonas, Lago do Rei.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas: Lago do Rei, Abends an bord bei Licht, 28-IX-1959, leg. Sioli-Settler (ZS). **Paratypes** (152): 132 males, 20 females, same data as holotype (ZS). Holotype to be deposited in IN; paratypes in ZS, JE.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella and distinctive superior volsella will distinguish the male of this species. The immature stages are unknown.

ETYMOLOGY. From the Latin *demissus,* hanging down, drooping; refers to the superior volsella when viewed laterally.

MALE IMAGO (n = 7)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with yellow-brown veins.

LENGTH. Total 3.73–4.10, 3.85 (4) mm. Thorax 0.97–1.01, 0.99 (4) mm. Abdomen 2.73–3.15, 2.90 (6) mm.

HEAD. Setae: temporal 31-37, 36 (4); clypeal 15–21, 18 (6); cibarial 7–10, 9 (4). Palpomere lengths: 33–40, 38; 40–52, 46; 85–108, 97; 100–118, 111; 180–198, 189 (6). Frontal tubercles 20–28, 24 long, 8–10, 9 wide (5). AR 1.87–2.18, 1.96 (6).

THORAX. Scutal tubercle well developed; humeral pit 3–12 small to moderate tubercles. Acrostichals 5–12, 8; dorsocentrals 14–20, 18; scutellars 8–10, 9 (6); prealars 9–12, 10.

WING. Length 1.55–1.68, 1.63 mm (6); width 0.46–0.50, 0.48 (6) mm. FCu distal to RM. VR 0.85–0.87, 0.88 (5). Setae: brachiolum 2–3, 2; squama 2–3, 2; R 13–18, 15; R_1 5–10, 8; R_{4+5} 6–13, 10.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 10–13, 11 on middle metatarsus, 7–11, 9 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	880-960, 907	760-790, 773	855-890, 874
ti	580-625, 601	670-695, 685	870-910, 900
ta_1	1070-1100 (2)	380-410, 401	580-610, 589
ta_2	510-520 (2)	190-210, 203	295-310, 304
ta_3	440-450 (2)	135-155, 145	234-245, 240
ta_4	390-395 (2)	55-60, 59	120-130, 124
ta_5	180 (2)	60-70, 65	90-100, 96
LR	1.75-1.82 (2)	0.57-0.60, 0.59	0.64-0.68, 0.66
BV	1.69-1.70 (2)	3.78-4.10, 3.94	3.01-3.18, 3.10
SV	1.37-1.42 (2)	3.52-3.79, 3.63	2.92-3.10, 3.01

ABDOMEN. 5 ventral accessory setae on S VI.

HYPOPYGIUM (Figs. 19A, B) with 4–8, 6 medial setae. Gonostylus apically expanded, curved medially, with 5–6 preapical setae. Superior volsella (Fig. 19C) length 78–95, 85 (5); width 13–18, 16 (5); LWR 4.9–6.2, 5.5; elongate-cylindrical with pointed apex and a dorsal basal lobe from which volsella is suspended; dorsal portion with 2–3 sensilla chaetica, elongate suspended portion with 1 sensilla chaetica. Inferior volsella length 140–163, 153 (6); deeply bifid, with 2–4 sensilla chaetica in single row on proximal lobe, 2–5 sensilla chaetica in single row on distal lobe; distal lobe with 1 well developed ventral preapical seta. Anal point bare dorsally; with 3–6, 4 dorsal basal setae and 4–8, 6 lateral basal setae.

FEMALE IMAGO (n = 3)

COLOR (slide mounted specimens). Similar to male.

LENGTH. Total 3.28–3.84, 3.58mm. Thorax 1.08–2.63, 1.18 mm. Abdomen 2.20–2.58, 2.40 mm.

HEAD. Setae: temporal 31–41, 36; clypeal 27–33, 30; cibarial 5–10, 8. Palpomere lengths: 40–48, 44; 48–55, 52; 85–108, 97; 100–118, 111; 180–198, 189 (6). Frontal tubercles 12–15, 13 long, 11–17, 14 wide. AR 0.46–0.56 (2).

THORAX. Scutal tubercle well developed; humeral pit with 1 small tubercle. Acrostichals 11–14, 12; dorsocentrals 27–38, 31; scutellars 12–14, 13; prealars 10–12, 11.

WING. Length 1.76–1.94; 1.88 mm; width 0.60–0.68, 0.64 mm. FCu distal to RM. VR 0.83–0.85, 0.84. Setae: brachiolum 2–3, 2; squama 6–9, 7; R 24–31, 26; R_1 15–18, 16; R_{4+5} 23–28, 26.

LEGS. Palmate sensilla chaetica: 18–21, 20 on middle metatarsus, 16–18, 17 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	910-1015, 975	780-960, 867	910-1000, 970
ti	630-705, 677	715-885, 787	940-1035, 1002
ta_1	—	430-465, 448	580-660, 627
ta_2	—	205-215, 208	295-320, 308
ta_3	—	140-150, 147	240-260, 250
ta_4	—	70	120-140, 132
ta_5	—	80	95-105, 102
LR	—	0.53-0.60, 0.57	0.62-0.64, 0.63
BV	—	3.89-4.49, 4.16	3.24-3.31, 3.28
SV	—	3.48-3.97, 3.68	3.08-3.19, 3.15

ABDOMEN. 2–8 ventral accessory setae on S VI. Notum 190–193, 191; cerci 110–130, 119. S VIII with 25–28, 27 setae/side; X with 8–9, 8 setae; Gc IX with 2–3, 3 setae/side. DmL, VlL and ApL as in Fig. 19D.

Dicrotendipes fittkaui sp. nov. (Figs. 20, 21)

TYPE LOCALITY: Brazil, Reserva Duke nr Manaus.

TYPE MATERIAL: **Holotype:** male/Pex, BRAZIL, Amazonas: Reserva Duke, nr Manaus, reared from a ground water puddle in the forest, 9-10-V-1961, leg. E.J. Fittkau (ZS). **Paratypes** (9): Brazil, Amazonas, Lago do Calado, from vegetation in central part of floating meadow, 10-VIII-1968, leg. W. Junk, 1 pharate male pupa (ZS); Lago do Calado, lower Rio Solimões,

nr village Manacapurú, experimental box filled with wood wool as artificial substrate, exposed free floating at border of marginal floating meadows, Autumn 1968, leg. W. Junk, 1 pharate male pupa (ZS); Lago Cabaliana, lower Rio Solimões, drift, leg. F. Reiss, 1 male (ZS). Pará: Alemquer, no porto, as 20 horas, na luz, 15-VII-1946, leg. Sioli, 4 males (ZS); Rio Cururú, Missão Cururú, right tributary of Rio Tapajós, light trap, 16-I-1961, leg. E.J. Fittkau, 2 males (ZS); same locality & collector, 19-I-1961, 1 male (ZS). Holotype to be deposited in IN; paratypes in ZS, JE.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella, distinctive superior volsella, clavate gonostylus and bulbous swelling beneath the anal point will distinguish this species. The female and larva are unknown.

ETYMOLOGY. I take great pleasure in naming this species in honor of Prof. Dr. E.J. Fittkau.

MALE IMAGO (n = 6)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with yellow-brown veins.

LENGTH. Total 3.13–3.45, 3.32 (4) mm. Thorax 0.78–0.96, 0.85 (4) mm. Abdomen 2.35–2.65, 2.46 (5) mm.

	P_1	P_2	P_3
fe	820-850, 835 (4)	700-745, 721 (5)	770-810, 796 (4)
ti	520-560, 532 (5)	630-665, 646 (5)	810-830, 820 (2)
ta_1	1090-1140 (2)	350-360, 354 (5)	530-540, 533 (3)
ta_2	480-550 (2)	170-190, 179 (5)	250-270, 260 (3)
ta_3	400-485 (2)	115-130, 122 (5)	190-210, 202 (3)
ta_4	355-430 (2)	55-60, 57 (5)	100-110, 105 (3)
ta_5	160-175 (2)	55-60 58 (5)	80-85, 82 (3)
LR	2.06-2.19 (2)	0.54-0.57, 0.55 (5)	0.64-0.66, 0.65 (3)
BV	1.53-1.76 (2)	4.02-4.22, 4.14 (5)	3.22-3.39, 3.31 (3)
SV	1.20-1.25 (2)	3.71-3.92 3.86 (5)	3.00-3.08, 3.03 (3)

HEAD. Setae: temporal 29–35, 32 (4); clypeal 8–13, 12; cibarial 2–11, 8 (4). Palpomere lengths: 30–50, 37 (4); 38–45, 42 (4); 70–95, 81 (4); 105–115, 108 (3); 175–178, 177 (3). Frontal tubercles 8–20, 13 long, 5–8, 7 wide. AR 1.84–2.08, 1.94 (5).

THORAX. Scutal tubercle well developed; humeral pit 1–3 moderate tubercles. Acrostichals 6–11, 8 (5); dorsocentrals 15–20, 17 (4); scutellars 8–11, 9 (4); prealars 7–10, 9 (4).

WING. Length 1.30–1.55, 1.47 mm (5); width 0.37–0.43, 0.41 mm (5). FCu distal to RM. VR 0.86–0.89, 0.88 (5). Setae: brachiolum 2–3, 2; squama 1–3, 2 (5); R 14–18, 16 (5); R_1 7–9, 8 (5); R_{4+5} 7–15, 12 (5).

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 7–13, 10 (5) on middle metatarsus, 3–7, 5 (3) on hind metatarsus. Lengths and proportions of legs on p. 71.

ABDOMEN. Ventral accessory setae on S VI not apparent.

HYPOPYGIUM (Figs. 20A, B) with 3–7, 5 medial setae. Gonostylus apically expanded, curved medially, with 6–10 preapical setae. Superior volsella (Fig. 20C) length 45–58, 53 (3); width 33–43, 37 (3); LWR 1.3–1.7, 1.4 (3); semi-pediform, with ventral subapical lobe; with dorsal and ventral fine setae; with 1–4 small sensilla chaetica. Inferior volsella length 125–154, 142 (5); deeply bifid, with 3–5 sensilla chaetica in single row on proximal lobe, 5–6 sensilla chaetica in single row on distal lobe; distal lobe with 1 well developed ventral preapical seta. Anal point bare dorsally, with basal peduncle and bulbous ventral extension, deflexed; with 0–2 dorsal basal setae and 8–14, 10 lateral basal setae.

PUPA (n = 3)

COLOR. Clear with light brown margins.

LENGTH. Total 3.40 mm (1). Cephalothorax 0.42 mm (1). Abdomen 2.98–3.40, 3.20 mm.

CEPHALOTHORAX. Cephalic tubercles (Fig. 21A) 40–50 (2) high, 68–83 (2) wide. Dorsum moderately smoothly pebbled. Dc_2 closer to Dc_3. Thoracic horn base (Fig. 21B) with tracheal bundles separate.

ABDOMEN (Fig. 21C). Sternites I-IV with fine lateral shagreen bands; S V-VI with posterior areas of fine shagreen. Tergite I sometimes with small scattered posterolateral spinules; T II with T-shaped shagreen area, spinules largest posteriorly; T III-V with median quadrilateral shagreen area; T VI with triangular shagreen area, spinules largest mesally; T VII with an anterior pair of small ovoid shagreen areas; T VIII with a pair of longitudinal fine shagreen bands. Tergites IV and V with a posterior band of fine spinules; T V-VI with posterolateral group of fine spines. Posterior margin of T II with transverse row of 65–72, 68 hooklets. T VIII with 4 lateral lamellar setae. Caudolateral spurs on T VIII (Figs. 21D, E) single or double, moderately large. Anal lobes with 39–52, 46 setae. DR 1.69–2.09, 1.93.

Dicrotendipes palearivillosus sp. nov. (Fig. 22)

TYPE LOCALITY: Costa Rica, San Jose Queb. Muerte.

TYPE MATERIAL: **Holotype:** male, COSTA RICA: San Jose Queb. Muerte, route 2, 3.5 km (air) W Villa Mills, 9.652 N, 83.743 W, 12.vi.1986, el. 3120 m, Holzenthal, Heyn, Armitage (CU). **Paratypes** (2): same data as holotype, 1 male (CU); Heredia, Est. Biol. La Selva, Rio Puerto Viejo, 10.440 N, 84.012 W, 19-VI-1986, el. 30 m, Holzenthal, Heyn, Armitage, 1 male (CU). The holotype will be deposited in the US, one paratype in CU and the other in JE.

DIAGNOSIS: The immaculate wings, distinctive digitiform superior volsella with small membranous ventral basal lobe and simple inferior volsella will distinguish this species. The female and immature stages are unknown.

ETYMOLOGY. From the Latin *palear,* a flap or wattle, and *villosus,* hairy; refers to the basal lobe of the superior volsella.

MALE IMAGO (n = 2)

COLOR (slide mounted specimens). Head and body light yellow-brown (probably green in life); fore femora greenish-stramineous, apex of femur and remainder of leg light brown, mid and hind legs greenish-stramineous, apical tarsomeres darker. Wing immaculate, slightly dusky brown, with light yellow-brown veins.

LENGTH. Total 3.38–3.73 mm. Thorax 0.88–0.90 mm. Abdomen 2.50–2.83 mm.

HEAD. Setae: temporal 33–35; clypeal 18–20; cibarial 5–6. Palpomere lengths (1): 43; 43; 113; 143; 210. Frontal tubercles 2–4 long, 2–3 wide. AR 2.06–2.07.

THORAX. Scutal tubercle well developed; humeral pit indiscernible. Acrostichals 5–6; dorsocentrals, 15–17; scutellars 7–10; prealars 8–9.

WING. Length 1.70–1.73 mm; width 0.48–0.50 mm. FCu distal to RM. VR 0.87–0.89. Setae: brachiolum 2–3; squama 4–5; R 19; R_1 8–11; R_{4+5} 15–22.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 4–8 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	880-930	760-790	850-885
ti	760-680	700-710	920-940
ta_1	1190-1290	380-390	630-645
ta_2	530-540	200-210	295-310
ta_3	455-460	140	230
ta_4	400-410	70	120-130
ta_5	175-185	55-60	75-90
LR	1.78–1.90	0.54–0.55	0.68–0.69
BV	1.76–1.82	3.94–3.96	3.25–3.33
SV	1.25–1.30	3.84–3.85	2.81–2.83

ABDOMEN. 3–5 ventral accessory setae on S VI; one specimen with 1 ventral accessory seta on S VII.

HYPOPYGIUM (Fig. 22A) Gonostylus moderate, curved medially, with 4–5 preapical setae. Superior volsella (Fig. 22B) length 67–68, width 16–18; digitiform with bare, apparently slightly membranous apex and with basal membranous ventral lobe or flap covered with long, fine setae; with 4–6 ventromedial sensilla chaetica. Inferior volsella length 110–113; simply clubbed; with 3–4 dorsal sensilla chaetica in 2 rows, with 1 well developed ventral preapical seta. Anal point bare dorsally, on small peduncle, slightly deflexed; with 3–4 dorsal basal setae and 8 lateral basal setae.

Dicrotendipes paradasylabidus sp. nov. (Fig. 23)

TYPE LOCALITY: Brazil, Amazonas, upper Rio Solimões at mouth of Rio Takana.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas: upper Rio Solimões at the mouth of Rio Takana (west of Rio Ica), light trap, 15-VIII-1961, leg. E.J. Fittkau (ZS). Holotype to be deposited in IN.

DIAGNOSIS: The immaculate wings, stout, deeply bifid and densely setose inferior volsella, distinctive bifid superior volsella and cordiform-emarginate base of the anal point will distinguish this species. Its small size and lack of sensilla chaetica on the ventral portion of the bifid superior volsella will distinguish this species from *D. dasylabidus.*

ETYMOLOGY. From the Greek *para,* near, *dasys,* hairy and *labidos,* forceps; refers to the inferior volsella and the apparent close relationship between this species and *D. dasylabidus.*

MALE IMAGO (n = 1)

COLOR (slide mounted specimen). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with light brown veins.

LENGTH. Total 2.95 mm. Thorax 0.75 mm. Abdomen 2.20 mm.

HEAD. Setae: temporal about 30; clypeal 11; cibarial indiscernible. Palpomere lengths: 35; 35; 75; 102; 177. Frontal tubercles 5 long, 6 wide. AR 1.79.

THORAX. Scutal tubercle well developed; humeral pit indiscernible. Acrostichals 8; dorsocentrals 18; scutellars 8; prealars 10.

WING. Length 1.35 mm; width 0.39 mm. FCu distal to RM. VR 0.86. Setae: brachiolum 2; squama 1; R 14; R_1 5; R_{4+5} 7.

LEGS. Foretarsi missing. Palmate sensilla chaetica: 7 on middle metatarsus, 2 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	740	620	700
ti	470	545	720
ta_1	—	340	465
ta_2	—	160	230
ta_3	—	110	180
ta_4	—	45	90
ta_5	—	50	70
LR	—	0.62	0.65
BV	—	4.12	3.31
SV	—	3.43	3.05

ABDOMEN. 2 ventral accessory setae on S VI.

HYPOPYGIUM (Fig. 23A) with 17 dorsomedial setae. Gonostylus thin, slightly curved medially, with 3 preapical setae. Superior volsella (Fig. 23B) bifid; length of dorsal portion 42, ventral portion 49; width of dorsal portion 11, ventral portion 25; dorsal portion small, digitiform, sclerotized, with 2 sensilla chaetica; ventral portion thin, lamellar, densely setose, without sensilla chaetica. Inferior volsella length 133; deeply bifid, stout, with 4 sensilla chaetica each on proximal and distal lobes, densely setose on inner margin, with 2 well developed ventral preapical setae. Anal point cordiform-emarginate basally, bare dorsally; with 6–8 lateral basal setae.

Dicrotendipes paterjohni sp. nov. (Fig. 24)

TYPE LOCALITY: Brazil, Amazonas, lower Rio Preto da Eva.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas: lower Rio Preto da Eva, left tributary of upper Rio Amazonas, village Tiririca, light trap, [no date], leg. E.J. Fittkau (ZS). Holotype to be deposited in IN.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella, distinctive pediform superior volsella and bulbous swelling beneath the anal point will distinguish this species.

ETYMOLOGY. From the Latin *father,* pater. I take pleasure in naming this species for "Father John" Kramer, whose assistance, both direct and indirect, has helped make this study possible.

MALE IMAGO (n = 1)

COLOR (slide mounted specimen). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with light brown veins.

LENGTH. Total 3.28 mm. Thorax 0.80 mm. Abdomen 2.73 mm.

HEAD. Setae: temporal indiscernible; clypeal 14; cibarial indiscernible. Palpomere lengths: 35; 40; 90; 117; 178. Frontal tubercles 10 long, 7 wide. AR 2.14.

THORAX. Scutal tubercle well developed; humeral pit indiscernible. Acrostichals 8; dorsocentrals 15; scutellars 8; prealars 9.

WING. Length 1.47 mm; width 0.40 mm. FCu distal to RM. VR 0.88. Setae: brachiolum 2; squama 2; R 16; R_1 6; R_4+_5 9.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 8 on middle metatarsus, 3 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	865	710	780
ti	510	625	800
ta_1	1180	360	510
ta_2	550	165	265
ta_3	475	110	205
ta_4	415	50	105
ta_5	170	50	75
LR	2.31	0.58	0.64
BV	1.59	4.52	3.22
SV	1.17	3.71	3.10

ABDOMEN. Ventral accessory setae on S VI not apparent.

HYPOPYGIUM (Fig. 24A) with 2 medial setae. Gonostylus apically expanded, slightly curved medially, with 6 preapical setae. Superior volsella (Fig. 24B) length 62; width 40; LWR 1.6; pediform, with 5 sensilla chaetica. Inferior volsella length 130; deeply bifid, with 4 sensilla chaetica each on proximal and distal lobes, with 1–2 well developed ventral preapical setae. Anal point bare dorsally; with basal peduncle and bulbous ventral extension; with 2 dorsal basal setae and 6–9 lateral basal setae.

Dicrotendipes radinovskyi sp. nov. (Fig. 25)

TYPE LOCALITY: Brazil, Amazonas, lower Rio Preto da Eva.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas: lower Rio Preto da Eva, left tributary of upper Rio Amazonas, village Tiririca, light trap, [no date], leg. E.J. Fittkau (ZS). **Paratypes** (2): same data as holotype, 2 males (ZS). Holotype to be deposited in IN, paratypes in ZS.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella, distinctive bifid superior volsella and bulbous swelling beneath the anal point will distinguish this species.

ETYMOLOGY. I take great pleasure in naming this species for my undergraduate mentor, Dr. Syd Radinovsky.

MALE IMAGO (n = 3)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, dusky brown, with brown veins.

LENGTH. Total 2.91–3.28, 3.07 mm. Thorax 0.73–0.80, 0.76 mm. Abdomen 2.18–2.48, 2.31 mm.

HEAD. Setae: temporal 29–34, 31; clypeal 12–14, 13; cibarial 6 (1). Palpomere lengths: 32–35, 33; 38–47, 43; 74–98, 89; 98–123, 114; 155–183, 168. Frontal tubercles 8–13, 11 long, 7–8, 8 wide. AR 1.85–1.92, 1.88.

THORAX. Scutal tubercle well developed; humeral pit with 6 medium tubercles. Acrostichals 6–7 (2); dorsocentrals 12–18, 15; scutellars 7–9, 8; prealars 8.

WING. Length 1.48–1.58, 1.52 mm; width 0.41–0.44, 0.43 mm. FCu distal to RM. VR 0.86–0.89, 0.88. Setae: brachiolum 2; squama 0(?)–4, 2; R 13–18, 15; R_1 4–8, 6; R_4+_5 10–13, 12.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 7–13, 9 on middle metatarsus, 3–4, 4 on hind metatarsus. Lengths and proportions of legs, p. 77.

ABDOMEN. 4–6 ventral accessory setae on S VI.

HYPOPYGIUM (Fig. 25A) with 2–3 medial setae. Gonostylus apically expanded, slightly curved medially, with 6 preapical setae. Superior volsella (Figs. 25B, C, D) bifid; length of dorsal portion 43–55, 51, ventral portion 53–80, 66; width of dorsal portion 15–21, 18, ventral portion 29–43, 36; dorsal portion digitiform with 2 sensilla chaetica, ventral portion expanded, with 3 sensilla chaetica. Inferior volsella length 138–151, 143; deeply bifid, with 4–5 sensilla chaetica on proximal lobe, 5–6 sensilla chaetica on distal lobe, with 2 well developed ventral preapical setae. Anal point bare dorsally; with triangular basal peduncle and bulbous ventral extension; deflexed; with 1–2 dorsal basal setae and 8–11 lateral basal setae.

Dicrotendipes reissi sp. nov. (Fig. 26)

TYPE LOCALITY: Paraná Madeirinha, lower Rio Madeira, Amazonas, Brazil.

TYPE MATERIAL: **Holotype:** male, BRAZIL: Amazonas, lower Rio Madeira, Paraná Madeirinha, light trap, 12-IX-1960, leg. E.J. Fittkau (ZS). **Paratypes** (212): same data as holotype, 202 males (ZS); Amazonas: Ilha do Careiro, upper Rio Amazonas, nr Manaus, Paraná

	P_1	P_2	P_3
fe	810–900, 847	690–750, 717	770–865, 808
ti	480–530, 500	600–675, 637	780–880, 822
ta_1	1110 (1)	340–390, 360	490–560, 522
ta_2	510 (1)	160–185, 168	245–280, 258
ta_3	440 (1)	105–110, 108	185–215, 197
ta_4	385 (1)	40–50, 47	85–105, 93
ta_5	185 (1)	50–55, 53	70–85, 78
LR	2.31 (1)	0.55–0.58, 0.57	0.61–0.66, 0.64
BV	1.58 (1)	4.52–4.59, 4.55	3.36–3.50, 3.44
SV	1.16 (1)	3.65–3.84, 3.76	3.01–3.26, 3.13

da Terra Nova at Careiro, ca. 2 km from mouth, light trap, 15-III-1961, leg. E.J. Fittkau, 1 male (ZS); lower Rio Preta da Eva, left tributary of upper Rio Amazonas, village Tiririca, light trap, [no date], leg. E.J. Fittkau, 7 males (ZS). Pará: Rio Cururú, Missão Cururú, right tributary of Rio Tapajós, 12-I-1961, leg. E.J. Fittkau, 1 male (ZS); same locality & collector, [no date], 1 male (ZS). Holotype to be deposited in IN; paratypes in ZS, JE.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella, distinctive superior volsella, clavate gonostylus and weakly cordiform-emarginate base of the anal point will distinguish this species. The female and immature stages are unknown.

ETYMOLOGY. I take great pleasure in naming this species in honor of Dr. F. Reiss, who has been so kind and helpful to me throughout my studies of the Chironomidae.

MALE IMAGO (n = 7)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, slightly dusky brown, with yellow-brown veins.

LENGTH. Total 2.93–3.28, 3.07 mm. Thorax 0.71–0.84, 0.77 mm. Abdomen 2.15–2.55, 2.39 mm.

HEAD. Setae: temporal 32–39, 36 (3); clypeal 11–14, 12; cibarial 7–10, 8 (5). Palpomere lengths: 27–38, 32 (6); 35–45, 38 (6); 80–101, 88 (6); 89–123, 107 (6); 150–203, 180 (5). Frontal tubercles 8–13, 11 long, 5–8, 6 wide. AR 1.72–2.00, 1.85.

THORAX. Scutal tubercle well developed; humeral pit with 3 moderate tubercles. Acrostichals 7–8, 8 (6); dorsocentrals 14–20, 17 (6); scutellars 7–9, 8 (6); prealars 8–10, 9 (6).

WING. Length 1.31–1.50, 1.41 mm; width 0.38–0.46, 0.41 mm. FCu distal to RM. VR 0.84–0.88, 0.86. Setae: brachiolum 2; squama 1–3, 2 (5); R 13–16, 14; R_1 4–7, 6; R_4+_5 8–12, 10.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 6–11, 9 on middle metatarsus, 3–6, 5 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	670–840, 776	580–690, 649	645–785, 729
ti	430–520, 489	495–615, 564	635–810, 741
ta_1	885–1105, 1009 (5)	300–370, 344	440–520, 483
ta_2	420–520, 473 (5)	145–180, 344	210–265, 239
ta_3	365–460, 412 (5)	100–135, 114	170–205, 189
ta_4	300–395, 350 (5)	40–60, 49 (6)	75–110, 89
ta_5	145–180, 159 (5)	45–55, 53 (6)	60–75, 67
LR	1.98–2.13, 2.06 (5)	0.59–0.63, 0.61	0.64–0.69, 0.65
BV	1.57–1.70, 1.63 (5)	3.90–4.32, 4.11 (6)	3.21–3.51, 3.35
SV	1.20–1.30, 1.25 (6)	3.44–3.68, 3.53	2.91–3.10, 3.04

ABDOMEN. 1–7 ventral accessory setae on S VI.

HYPOPYGIUM (Figs. 26A, B) with 14–30, 21 dorsomedial setae. Gonostylus apically expanded, curved medially, with 3–4, 3 preapical setae. Superior volsella (Figs. 26C, D) length 45–49, 47 (5); width 40–43, 41 (5); LWR 1.1–1.2, 1.1 (5); semi-pediform-triangular viewed dorsally, with ventral subapical extension; with dorsal and ventral fine setae; with 1–2 small sensilla chaetica. Inferior volsella length 118–135, 127 (5); deeply bifid, with 4–5 sensilla chaetica in single row on proximal lobe, 5–7 sensilla chaetica in single row on distal lobe; distal lobe with 1 well developed ventral preapical seta. Anal point weakly cordiform-emarginate basally, bare dorsally, with basal peduncle which slopes down from T IX; with 6–10, 8 lateral basal setae.

Dicrotendipes soccus sp. nov. (Fig. 27)

TYPE LOCALITY: Igarapé Paracaixi, left tributary of lower Rio Negro, some hours downstream from mouth of Rio Branco, Amazonas, Brazil.

TYPE MATERIAL: **Holotype:** male/Pex, BRAZIL: Amazonas: Igarapé Paracaixi, left tributary of lower Rio Negro, some hours downstream from mouth of Rio Branco, light trap, 14-II-1962, leg. E.J. Fittkau. **Paratypes** (42): Amazonas: lower Rio Madeira, Paraná Madeirinha, light trap, 11-IX-1960, leg. E.J. Fittkau, 31 males (ZS); same locality & collector, 12-IX-1960, 2 males (ZS); mouth of Rio Negro at Manaus, light trap, 17-III-1961, leg. E.J. Fittkau, 4 males (ZS); Upper Rio Solimões, Igarapé Amataura, ca. 50 km W mouth of Rio Ica, ca. 15 km from

mouth of Igarapé Amataura, light trap, 27-VIII-1961, leg. E.J. Fittkau, 1 male (ZS); Ilha do Careiro, upper Rio Amazonas, nr Manaus, Paraná da Terra Nova at Careiro, ca. 2 km from mouth, light trap, 15-III-1961, leg. E.J. Fittkau, 1 male (ZS); lower Rio Negro, Ponta Negra nr Manaus, light trap, 6-VI-1962, leg. E.J. Fittkau, 1 male (ZS); Rio Negro at Moura, light trap, 5-II-1962, leg. E.J. Fittkau, 1 male (ZS); Lago Cabaliana, lower Rio Solimões, drift, 16-VI-1971, leg. F. Reiss, 1 male (ZS). Holotype to be deposited in IN; paratypes in ZS, JE.

DIAGNOSIS: The immaculate wings, deeply bifid inferior volsella with greatly enlarged ventral subapical sensilla chaetica, distinctive slipper shaped superior volsella, clavate gonostylus and strongly cordiform-emarginate base of the anal point will distinguish this species. The female and larva are unknown.

ETYMOLOGY. From the Latin *soccus,* slipper; refers to the slipper shaped superior volsella.

MALE IMAGO (n = 7)

COLOR (slide mounted specimens). Head, body and legs light brown. Wing immaculate, light dusky brown, with yellow-brown veins.

LENGTH. Total 2.91–3.71, 3.28 (6) mm. Thorax 0.79–0.93, 0.84 (6) mm. Abdomen 2.11–2.80, 2.45 (6) mm.

HEAD. Setae: temporal 28–40, 35 (4); clypeal 9–14, 12 (6); cibarial 5–8, 7 (4). Palpomere lengths: 30–40, 34; 35–45, 41; 83–100, 90; 104–123, 113; 153–190, 179. Frontal tubercles 10 long, 5–7, 6 wide. AR 1.88–2.08, 1.99 (6).

THORAX. Scutal tubercle well developed; humeral pit with 3–5 weak to moderate tubercles. Acrostichals 7–10, 8; dorsocentrals 14–17, 16; scutellars 8–9, 9 (6); prealars 8–10, 8.

WING. Length 1.34–1.63, 1.46 mm; width 0.39–0.44, 0.42 mm. FCu distal to RM. VR 0.84–0.89, 0.86. Setae: brachiolum 2; squama 1–3, 2 (6); R 11–16, 14; R_1 2–7, 5; R_4+_5 3–15, 10.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 6–10, 8 on middle metatarsus, 3–5, 4 on hind metatarsus. Lengths and proportions of legs, p. 80.

ABDOMEN. 2–7, 5 ventral accessory setae on S VI.

HYPOPYGIUM (Figs. 27A, B) with 22–41, 30 dorsomedial setae. Gonostylus thin, slightly curved medially, with 2–3, 3 preapical setae. Superior volsella (Fig. 27C) length 50–65, 60; width 20–25, 22; LWR 2.3–3.1, 2.7; slipper shaped, with 2 preapical sensilla chaetica. Inferior volsella length 153–165, 155 (6); deeply bifid, with 3–6 sensilla chaetica in single row on proximal lobe, 4–6 sensilla chaetica in single row on distal lobe; distal lobe with 3–8 greatly developed ventral preapical setae; at least 3 of these setae usually larger than dorsal sensilla chaetica of same lobe. Anal point strongly cordiform-emarginate basally, bare dorsally, with basal peduncle which slopes down steeply from a squat T IX; with 4–8, 6 lateral basal setae.

PUPA (n = 1)

COLOR. Clear with pale yellow-brown margins.

LENGTH. Total 4.00 mm. Cephalothorax 0.95 mm. Abdomen 3.05 mm.

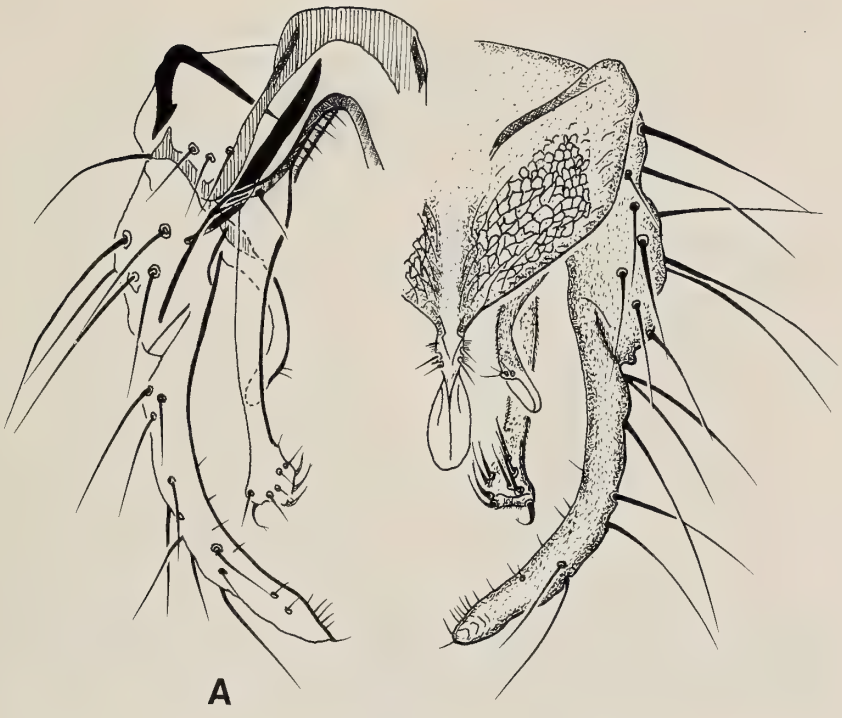
CEPHALOTHORAX. Cephalic tubercles similar to *D. fittkaui* (Fig. 20A), moderately developed. Dorsum moderately smoothly pebbled. Dc_2 closer to Dc_3. Thoracic horn base with tracheal bundles separate.

ABDOMEN. Similar to *D. fittkaui* (Fig. 21C). Sternites I-II with fine lateral shagreen bands, S I also with fine posterior shagreen; S III with scattered fine spinules; S VI with anterior and posterior areas of fine shagreen. Tergite I bare; T II with T-shaped shagreen area, spinules largest posteriorly; T III-V with median quadrilateral shagreen area; T VI with broadly tri-

	P_1	P_2	P_3
fe	725–895, 799	620–740, 671	715–840, 761 (6)
ti	470–585, 516	540–665, 599	740–870, 791 (6)
ta_1	960–1140, 1053 (6)	320–390, 352	440–540, 493 (6)
ta_2	450–530, 494 (6)	150–190, 170	220–270, 249 (6)
ta_3	385–470, 428 (6)	110–135, 121	180–210, 193 (6)
ta_4	340–410, 373 (6)	40–55, 49	80–100, 91 (6)
ta_5	150–180, 166 (6)	45–60, 53	70–80, 73 (6)
LR	2.04–2.18, 2.09 (6)	0.56–0.63, 0.59	0.59–0.67, 0.62 (6)
BV	1.53–1.63, 1.60 (6)	4.03–4.32, 4.15	3.32–3.43, 3.37 (6)
SV	1.18–1.26, 1.22 (6)	3.41–3.77, 3.61	2.93–3.31, 3.16 (6)

angular shagreen area, spinules largest mesally; T VII with an anterior pair of small ovoid shagreen areas; T VIII with a pair of longitudinal fine shagreen bands. Tergites IV and V with a posterior band of fine spinules; T V-VII with posterolateral group of fine spines. Posterior margin of T II with transverse row of 65 hooklets. T VIII with 4 lateral lamellar setae. Caudolateral spurs on T VIII similar to *D. fittkaui* (Figs. 21D, E) single or double, moderately large. Anal lobes with 38–39 setae. DR 2.08.

FIG. 13. *D. aethiops,* adult male. A) Hypopygium, dorsal/ventral. B–D) Variations of superior volsella, ventral.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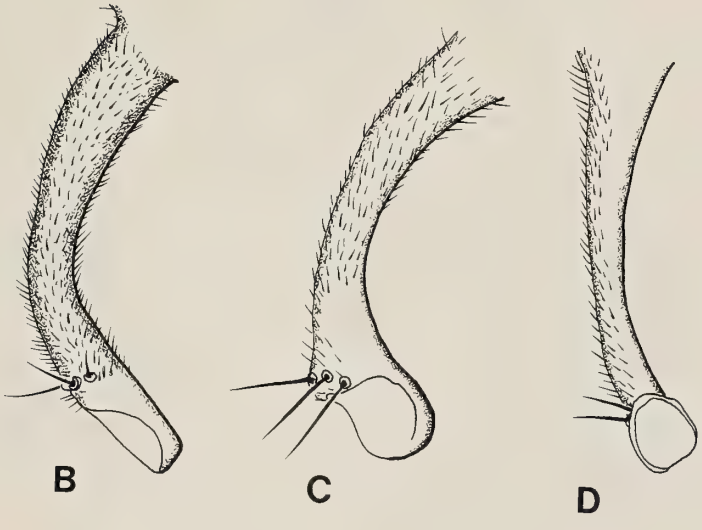

B
C
D

FIG. 14. *D. californicus,* adult male. A) Hypopygium, dorsal/ventral. B) Variation of anal point. C–D) Variations of superior volsella, ventral. E) Deformed superior volsella, ventral (Utah, U.S.A.).

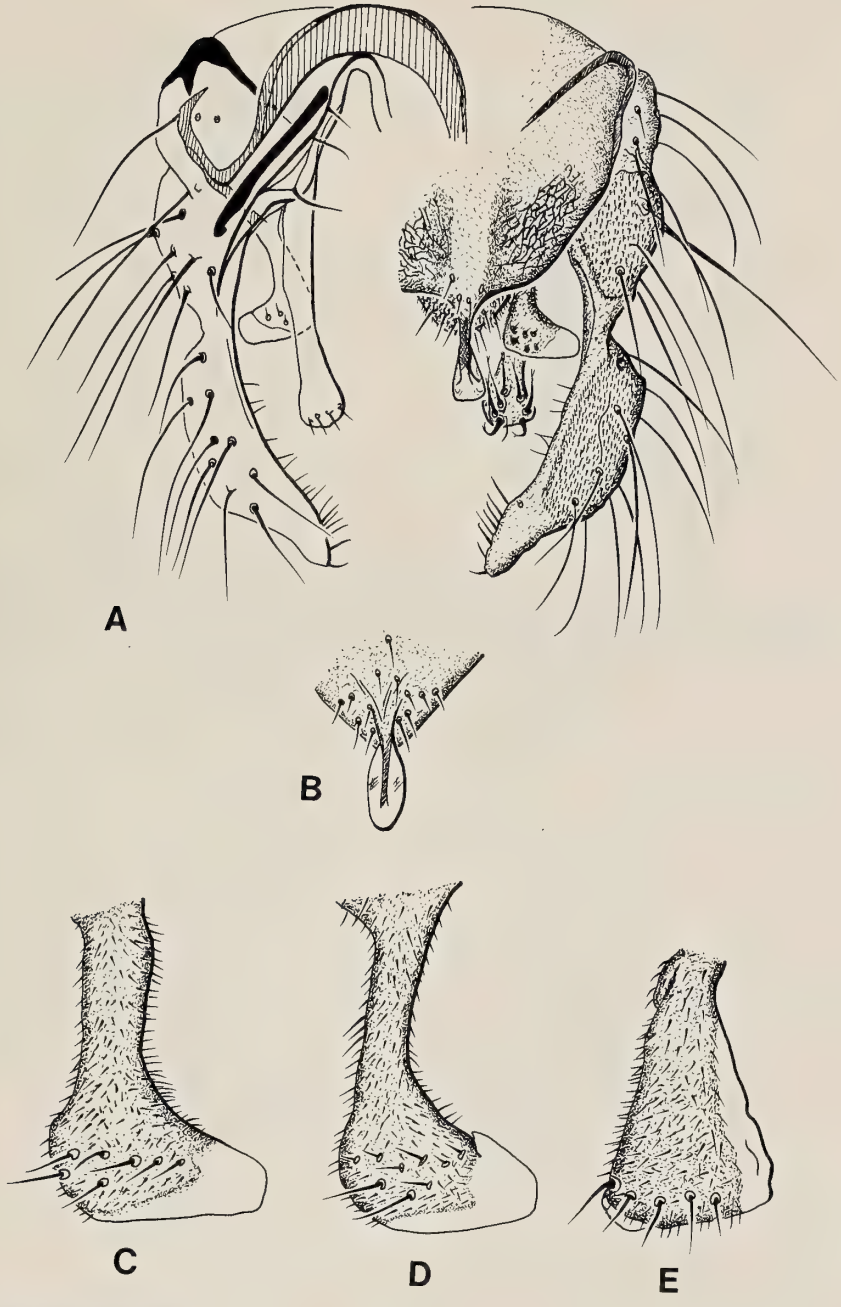
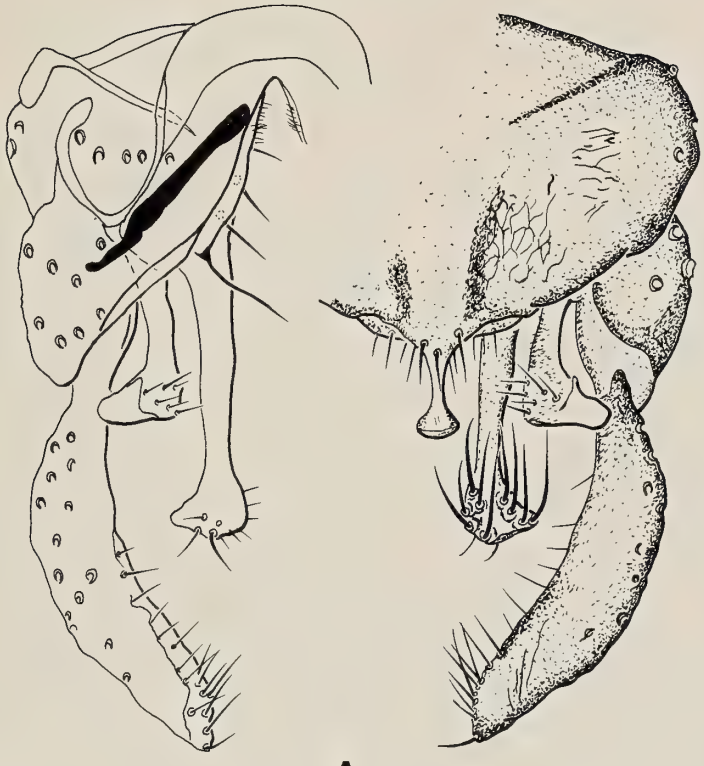
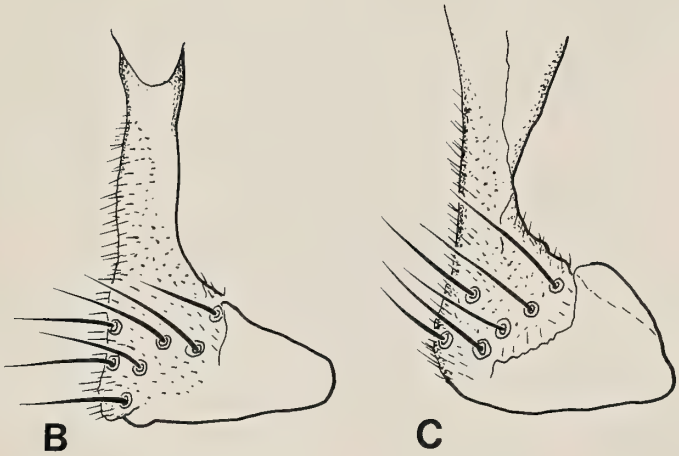

A
B
C
D
E

FIG. 15. *D. obrienorum,* adult male. A) Hypopygium, dorsal/ventral. B–C) Variations of superior volsella, ventral.

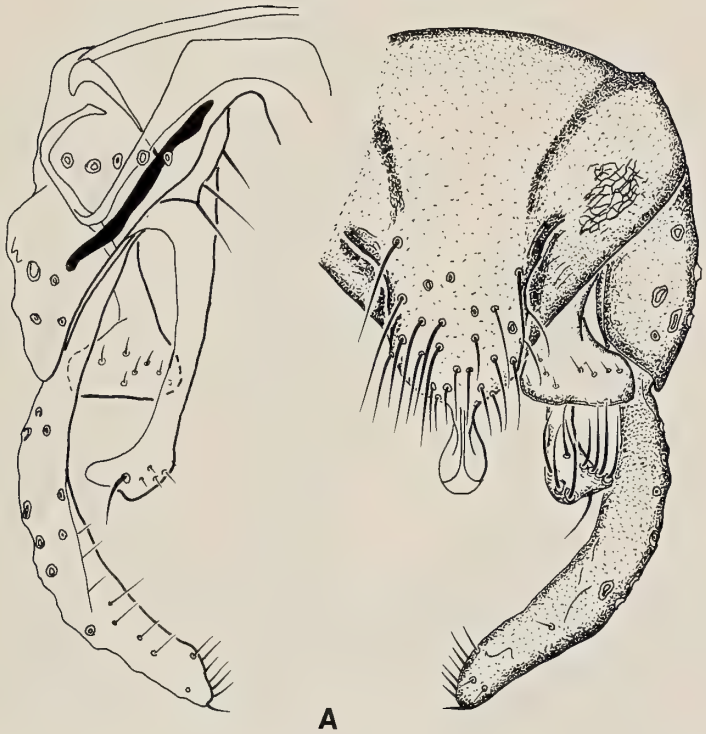


A



B C

FIG. 16. *D. sinoposus,* adult male. A) Hypopygium, dorsal/ventral. B) Superior volsella, ventral.



A

B

FIG. 17. *D. amazonicus,* adult male and female. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, lateral. D) Superior volsella, dorsal. E) Female DmL, ApL, VlL.

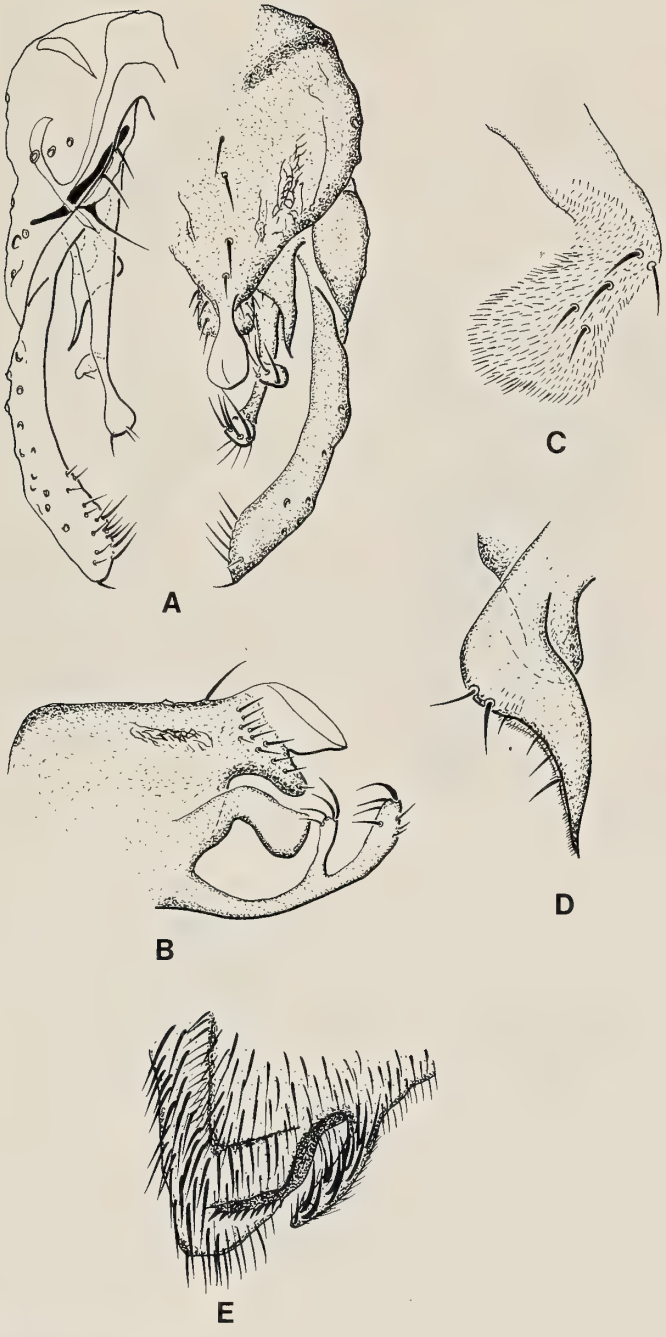

A
B
C
D
E

FIG. 18. *D. dasylabidus,* adult male. A) Hypopygium, dorsal/ventral. B) Superior volsella, dorsal.

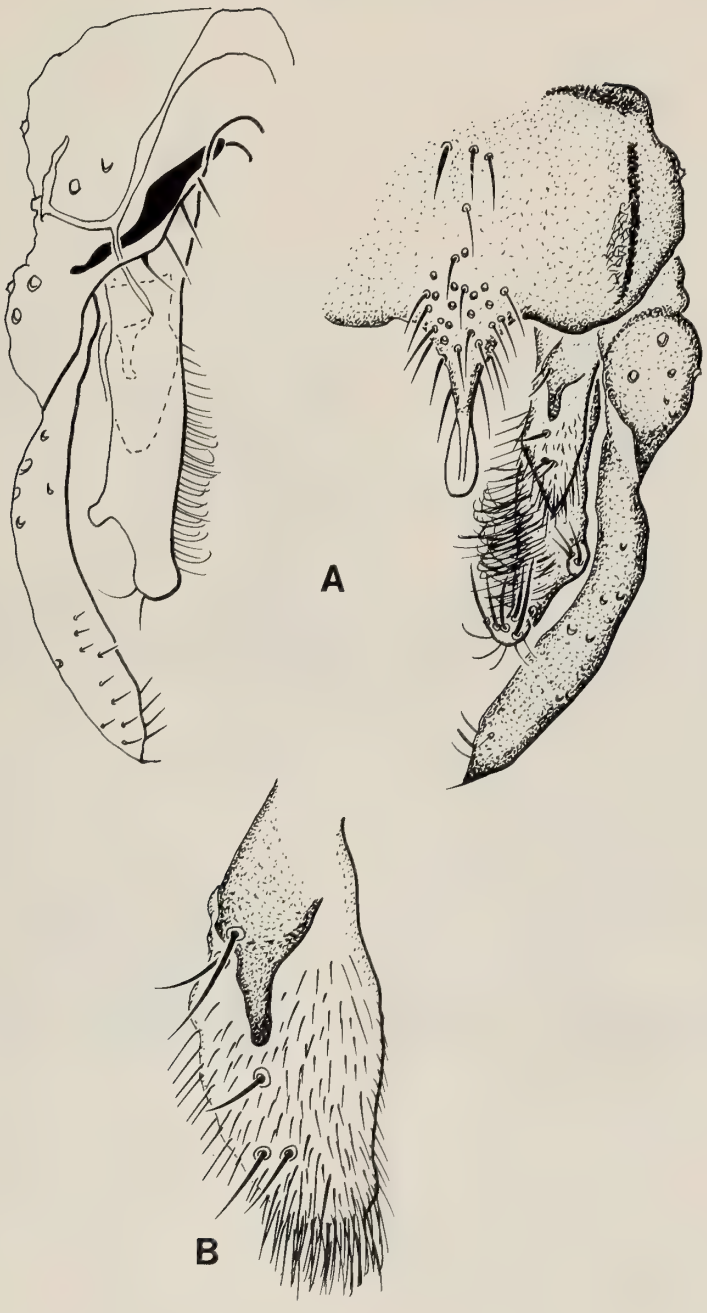

A
B

FIG. 19. *D. demissus,* adult male and female. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, dorsal. D) Female DmL, ApL, VlL.

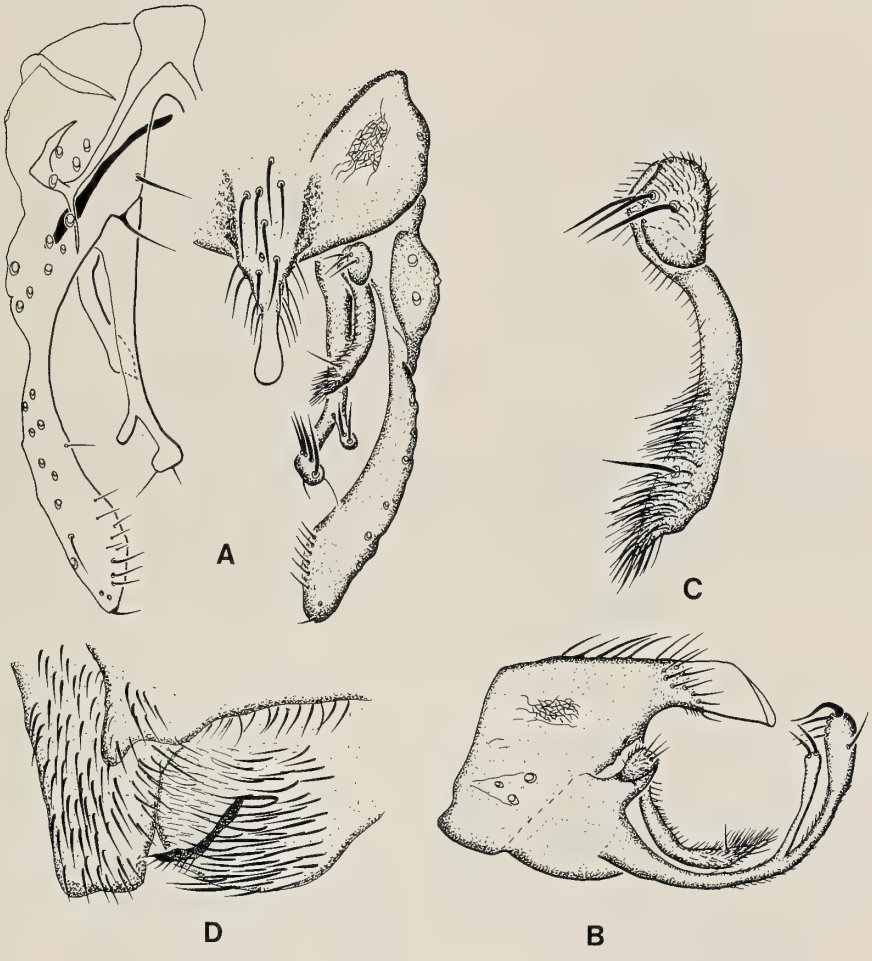

A
C
D
B

FIG. 20. *D. fittkaui,* adult male. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, ventral.

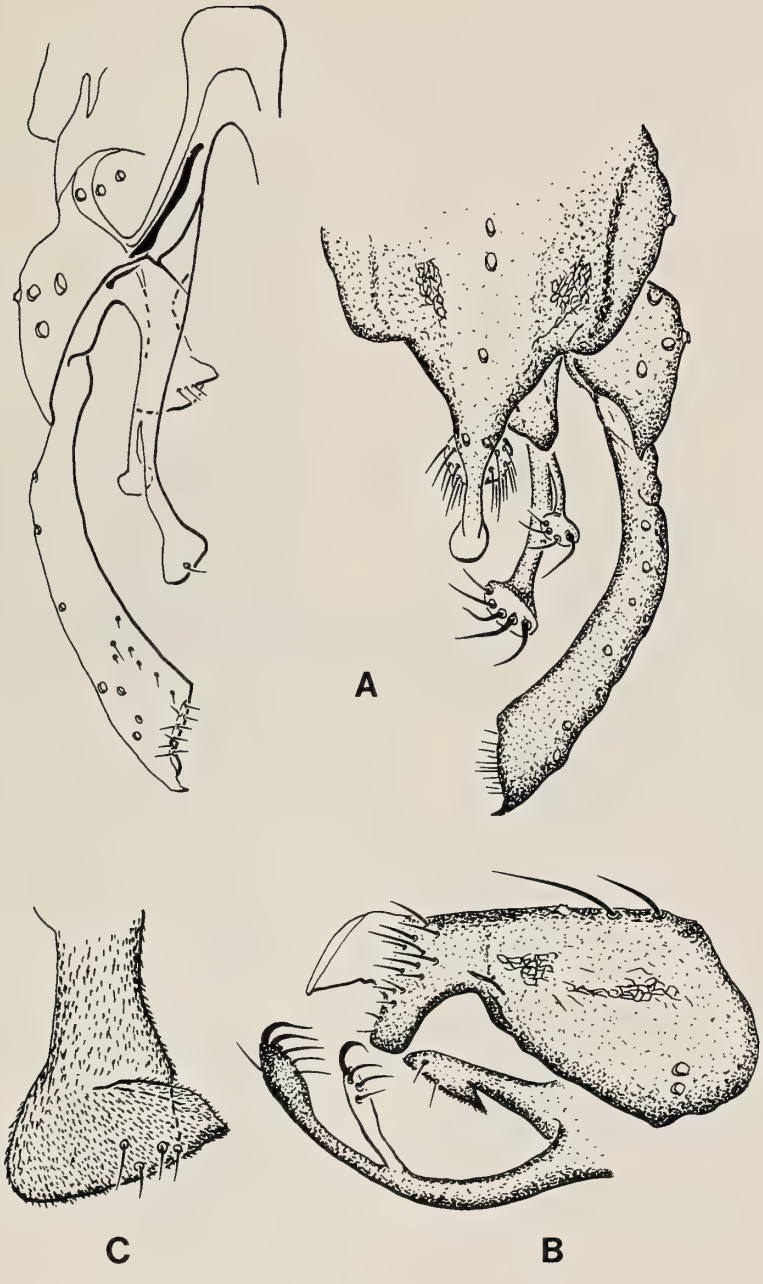

A
C
B

FIG. 21. *D.fittkaui,* pupa. A) Cephalic tubercles. B) Thoracic horn base. C) Abdomen, dorsal. D, E) Caudolateral spurs on T VIII.

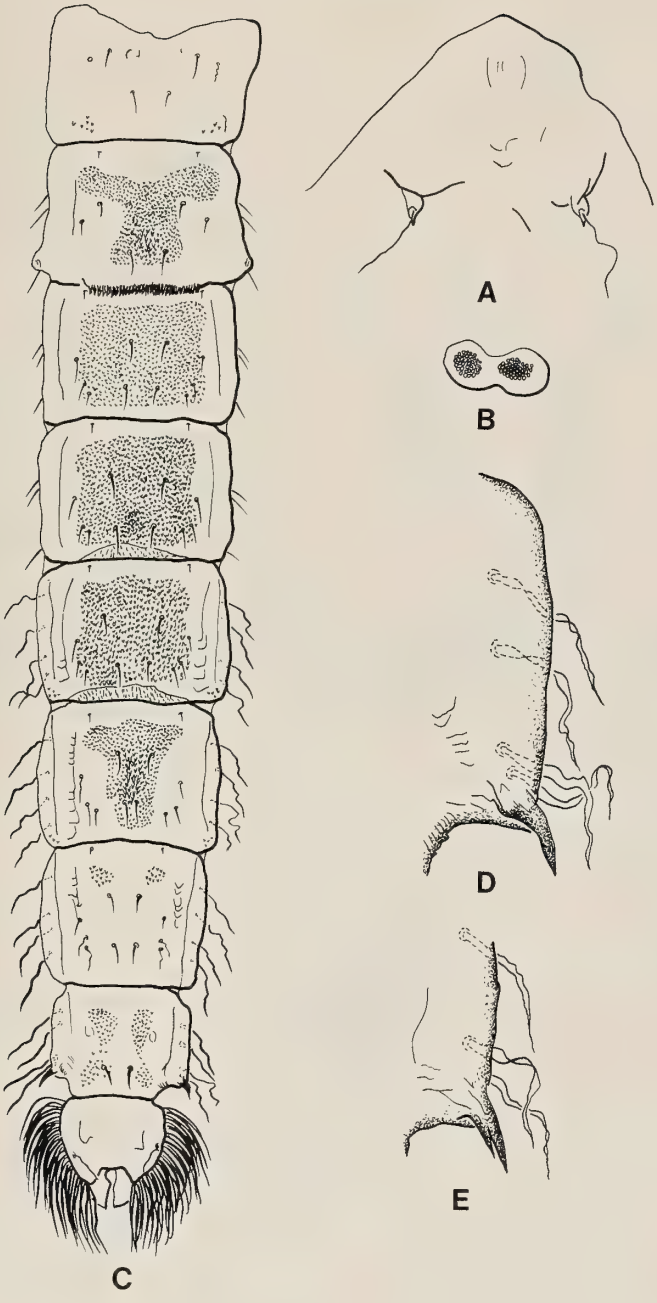
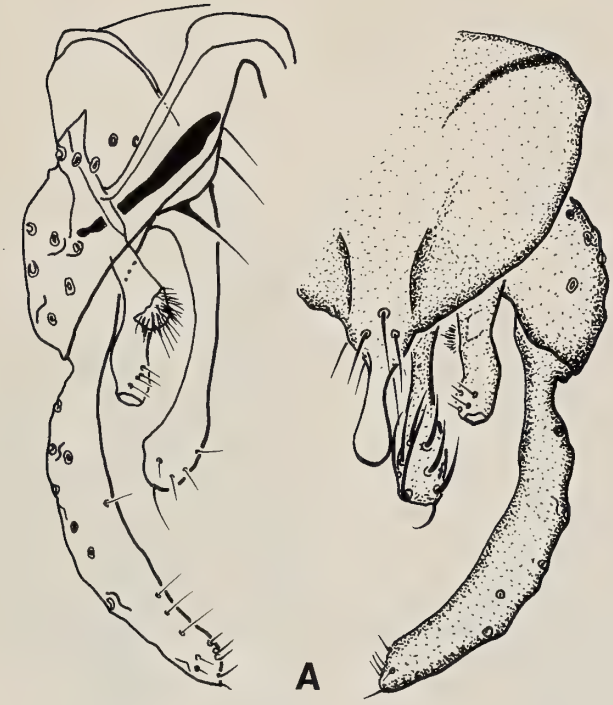

A
B
C
D
E

FIG. 22. *D. palearivillosus,* adult male. A) Hypopygium, dorsal/ventral. B) Superior volsella, ventral.


A

B

FIG. 23. *D. paradasylabidus,* adult male. A) Hypopygium, dorsal. B) Superior volsella, dorsal.

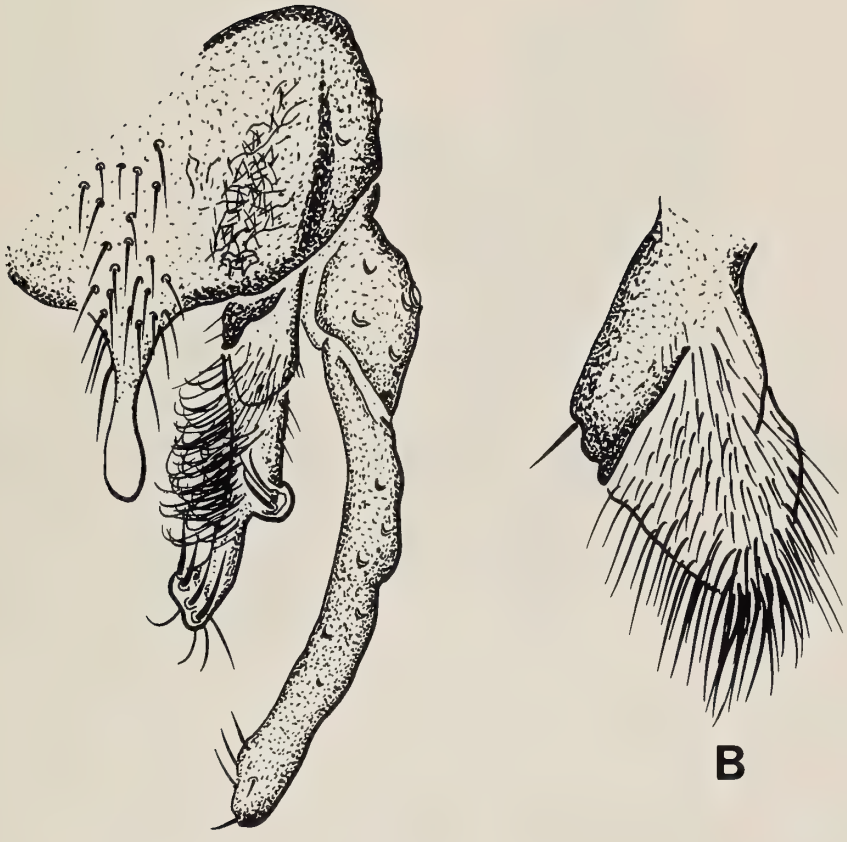
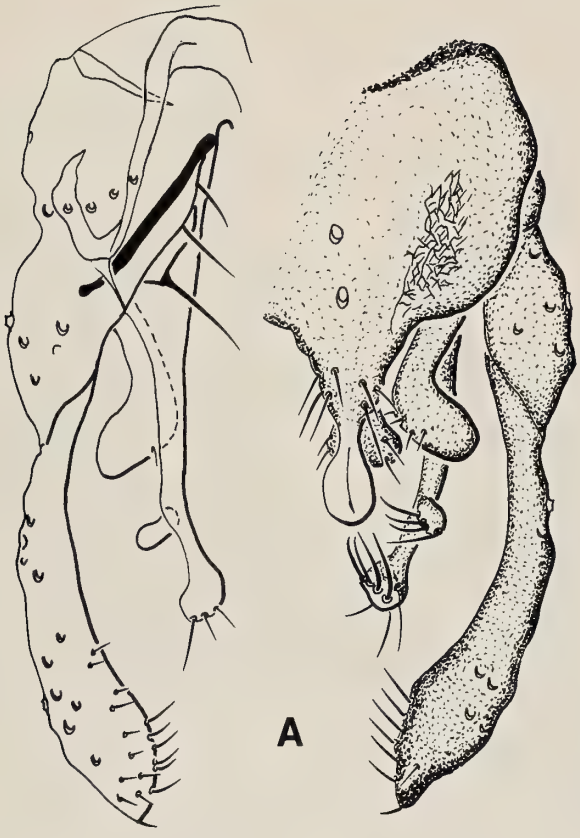

A
B

FIG. 24. *D. paterjohni,* adult male. A) Hypopygium, dorsal/ventral. B) Superior volsella, ventral.



A

B

FIG. 25. *D. radinovskyi,* adult male. A) Hypopygium, dorsal. B, C) Superior volsella, dorsal. D) Superior volsella, lateral.

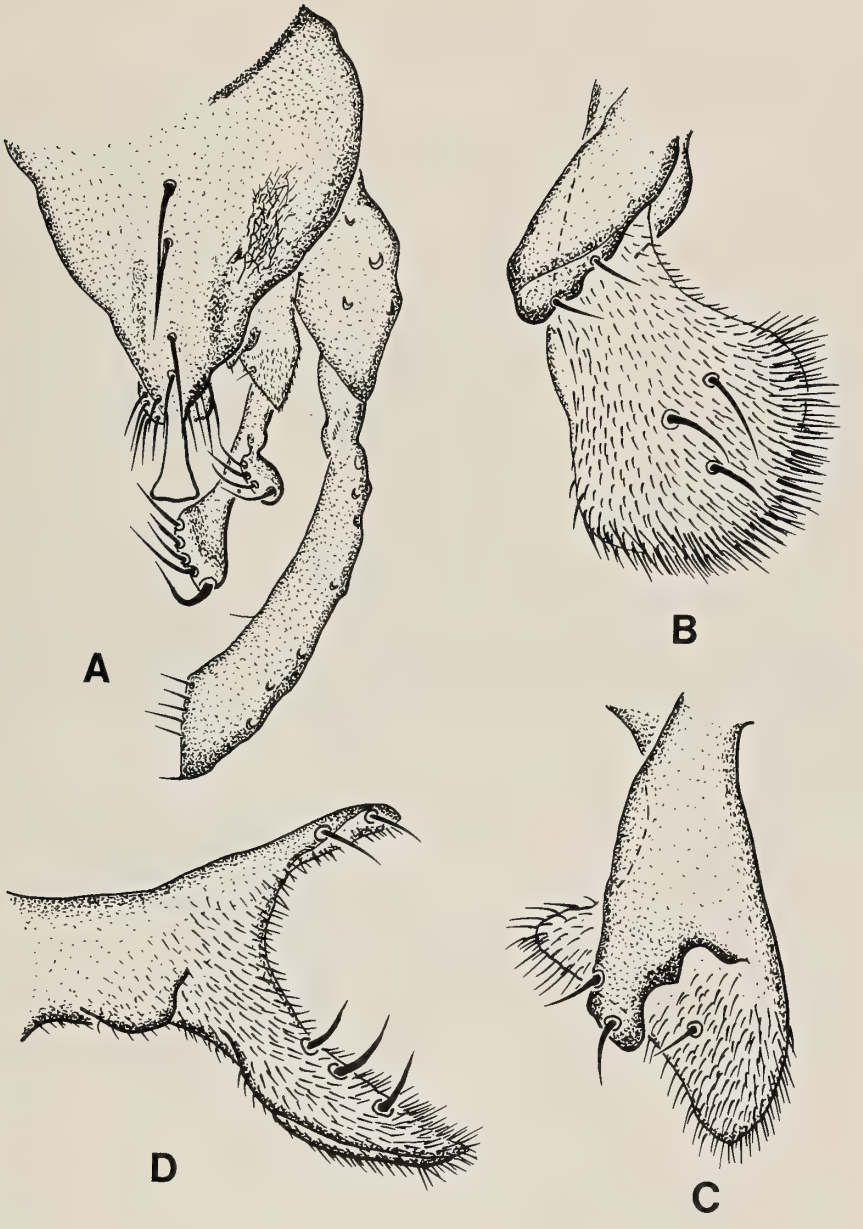

A
B
C
D

FIG. 26. *D. reissi,* adult male. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, dorsal. D) Superior volsella, lateral.

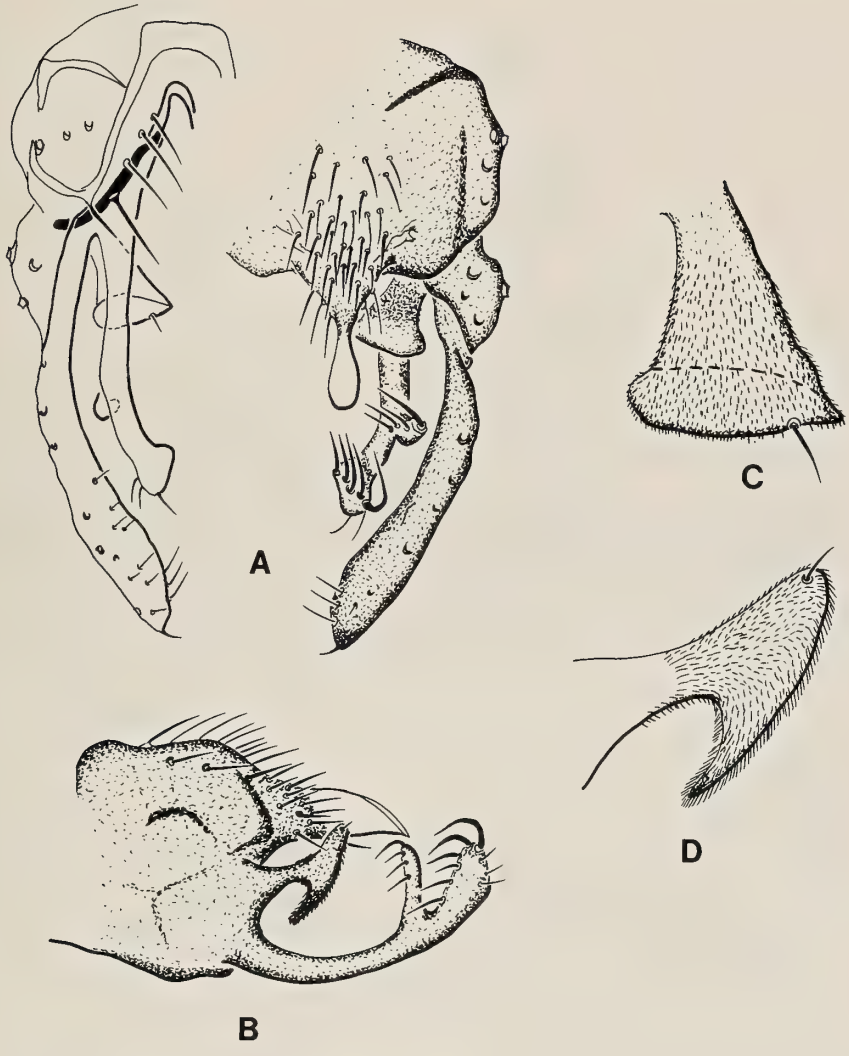
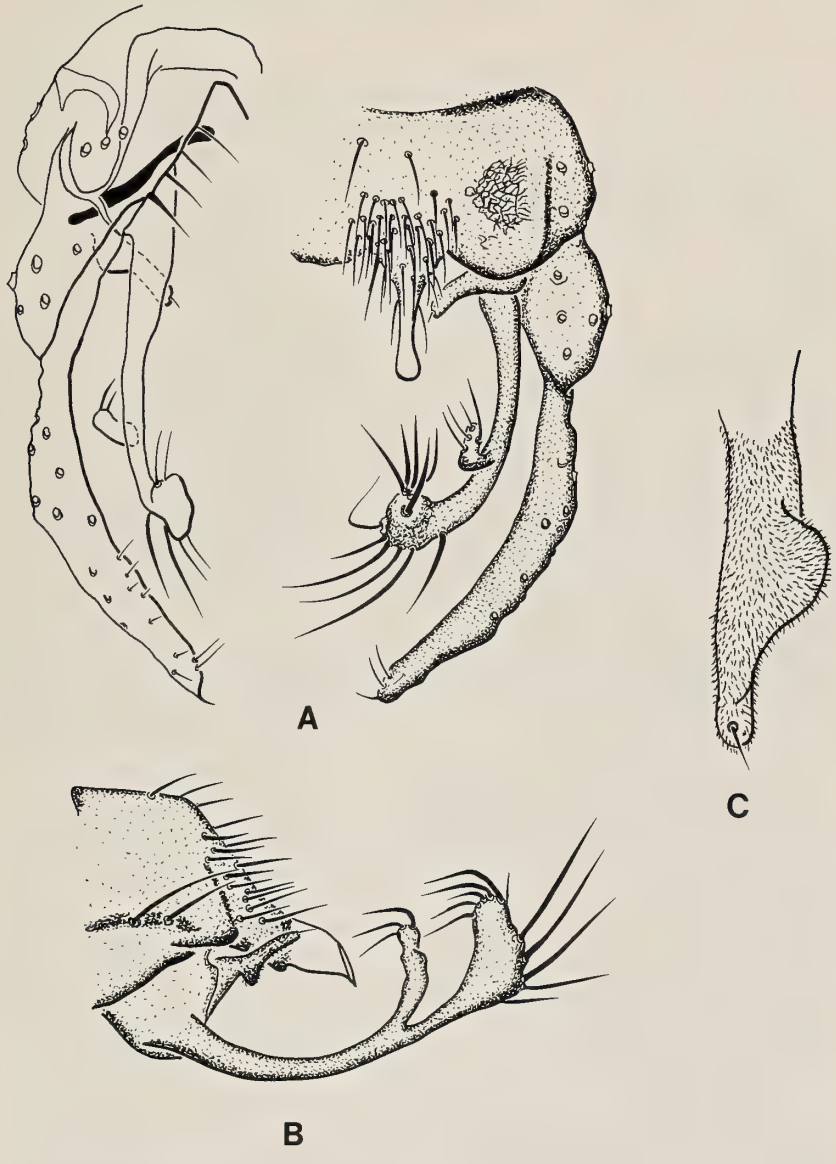

A
B
C
D

FIG. 27. *D. soccus,* adult male. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, dorsal.


A
B
C

Chapter IV
The *Dicrotendipes* of the Oriental-Australasian Region

The first species of *Dicrotendipes* described from the regions was named *Chironomus conjunctus* Walker (Walker 1856); Skuse (1889) merely repeated Walker's description. Kieffer also described several species from the regions in several papers (Kieffer 1910; 1911a; 1913a; 1916; 1917; 1921b). Edwards (1924; 1928) described 2 new species from Fiji and Samoa. Freeman (1961a) provided the first revision for the genus (as a subgenus of *Chironomus*) from the regions, describing 6 species from Australia, 4 of them new.

Chironomus (*Dicrotendipes*) *canterburyensis* Freeman was described from New Zealand from female specimens (Freeman 1959:425). Forsyth & McCallum (1978) reared this species (as an inquiline commensal) from a lammelibranch mussel, *Hydridella menziesi* (Gray), and on the basis of the immature stages, placed the species in *Xenochironomus* Kieffer. The genus *Dicrotendipes* remains unknown to me from New Zealand.

Sasa and Hasegawa (1983) provisionally described a species, *Dicrotendipes* sp. "Yaeyama," from Ishigaki Island in the Ryukyu Islands. The species appears to be related to the Holarctic *D. nervosus* group, not to *D. lobiger* as the authors stated. Specimens were not made available to me and it is not included in this study.

Two additional species of *Dicrotendipes* have been described from the region, *D. arcistylus* and *D. canitibialis* (Guha et al. 1985). These species are not included because they are insufficiently described and specimens were not made available. *Dicrotendipes arcistylus* may be a synonym of *D. flexus* or *D. tamaviridis* Sasa. *Dicrotendipes canitibialis* is variously spelled as *canitiibalis* and *canitibiatis* in Figure 5 and the text, respectively. Mention is made of 3 other species whose names are misspelled and/or misinterpreted: *D. conjunctus* (Walker) is misspelled as *conjuncts* and authorship of the species name is incorrectly attributed to Freeman; *D. incurvus* (Sublette), a Nearctic species, is apparently referred to as "*D. carllus*" (Guha et al. 1985:29); and *Chironomus* (*Prochironomus*) *punctatipennis* (a probable synonym of *D. septemmaculatus*) is misspelled as *D. punctipennis.*

In this study, I include 17 species from the combined Oriental-Oceanic-Australian regions. Three species previously considered to be *Dicrotendipes* are removed: *Ch. blandellus* Kieffer, 1906, (new name for *blandus* Skuse, 1889) is probably a *Chironomus* (see discussion under *D. conjunctus* below); *D. paxillus* Guha, Chaudhuri et Nandi, 1982, is a junior synonym of *Chironomus glauciventris* (Kieffer, 1912); and *D. socionotus* Guha, Chaudhuri

et Nandi, 1982, is probably a junior synonym of *Chironomus tainanus* (Kieffer, 1912). It should be noted that *Ch. tainanus* is also probably a senior synonym of *Nilodorum biroi* (Kieffer, 1918).

Key to Adult Males of Oriental-Australasian *Dicrotendipes*

[*D. arcistylus, D. canitibialis* and *D. semiviridis* not included]

1. Median volsella present (Figs. 28, 35) 2
   Median volsella absent 3
2. Median volsella short, squat (Fig. 28); wings immaculate . . . . *D. balciunasi* sp. nov.
   Median volsella long, thin (Fig. 35); wings marked with dark clouds and band. . . . . *D. lindae* sp. nov.
3. Inferior volsella with membranous dorsal extension (Fig. 34) 4
   Inferior volsella without membranous dorsal extension 5
4. Superior volsella pediform (Figs. 34A, B) . . . . . *D. jonmartini* sp. nov.
   Superior volsella digitiform (Figs. 34C, D) . . . . . *D. sarinae* sp. nov.
5. Anal point sharply deflexed, not visible in dorsal view (Figs. 29, 36) 6
   Anal point at most moderately deflexed, visible in dorsal view 7
6. Anal point long and narrow; inferior volsella with broad apical club; gonostylus of moderate width and dark brown in color (Fig. 29); wings immaculate . . . . . *D. bilobatus* (Kieffer)
   Anal point short and broad; inferior volsella with simple apex, not broadly clubbed; gonostylus broad and usually whitish to light brown (Fig. 36); wings sometimes with smoky highlights along major veins . . . . . *D. pelochloris* (Kieffer)
7. Wings with bands or spots 8
   Wings immaculate. 11
8. Wing with 6–7 spots; inferior volsella deeply bifid (Freeman 1961a:Fig. 20d). . . . . *D. septemmaculatus* (Becker)
   Wing with band of dark color; inferior volsella not deeply bifid (although dorsal sensilla chaetica may be widely separated in *D. leei* [Freeman 1961a:Fig. 20a]) 9
9. Superior volsella cylindrical-digitiform with weak membranous apex; Fiji and Samoa (Fig. 30) . . . . . *D. candidibasis* (Edwards)
   Superior volsella pediform or semi- pediform 10
10. Anal cell with spot; apex of superior volsella directed laterad; inferior volsella with dorsal sensilla chaetica only at or near apex (Freeman 1961a:Fig. 20b) . . . . . *D. taylori* (Freeman)
    Anal cell without spot; apex of superior volsella directed mesad; inferior volsella with widely separated rows of dorsal sensilla chaetica (Freeman 1961a:Fig. 20a). . . . . *D. leei* (Freeman)
11. Superior volsella slender, usually arched mesad; inferior volsella broad to extremely broad; medial setae originate from dorsal ovoid area on hypopygium. 12
    Superior volsella semi-pediform, weakly deltoid or long and slender, arched laterad; medial setae if present do not originate from dorsal ovoid area of hypopygium 14

12. Inferior volsella extremely broad (Fig. 32); acrostichal setae not present (setae-less pits present) . . . . . *D. cumberlandensis* sp. nov.
Inferior volsella not extremely broad (Fig. 31); acrostichal setae present 13

13. Superior volsella strongly arched mesad (Figs. 31D, E); foretarsal beard present. . . . . *D. pseudoconjunctus* sp. nov.
Superior volsella at most weakly arched mesad (Figs. 31A-C); foretarsal beard absent . . . . . *D. conjunctus* (Walker)

14. Superior volsella weakly deltoid, densely setose (Fig. 33) . . . . . *D. jobetus* sp. nov.
Superior volsella pediform-clubbed or long, slender and arched laterad, not densely setose 15

15. Superior volsella pediform-clubbed; distal portion not membranous, apex truncate (Fig. 37) . . . . . *D. tenuiforceps* (Kieffer)
Superior volsella thin, slender and arched laterad; distal portion membranous, apex not truncate (Johannsen 1932:Fig. 18; Hashimoto et al. 1981:Fig. 5D) (similar to Holarctic *D. nervosus*) . . . . . *D. flexus* (Johannsen)

Key to Known Pupae of Oriental-Australasian *Dicrotendipes*

1. T VII, VIII and anal lobe with extensive shagreen (Fig. 41B); S VIII with well-developed posterior shagreen band; cephalic tubercles minute. . . . . *D. flexus* (Johannsen)
T VII with at most an anterolateral pair of ovoid shagreen areas, T VIII with at most an anterior and posterior pair of ovoid shagreen areas or 2 longitudinal shagreen bands; anal lobe with or without shagreen; S VIII with faint shagreen; cephalic tubercles moderately to well developed 2

2. Posterior margin of T V with a row or groups of hooklets 3
Posterior margin of T V without hooklets 4

3. T V hooklets in 2 groups (Fig. 39K) . . . . . *D. conjunctus* (Walker); *D. pseudoconjunctus* sp. nov. (see text)
T V hooklets in continuous row (Fig. 42B) . . . . . *D. jonmartini* sp. nov.; *D. sarinae* sp. nov. (see text)

4. Anal lobe with dorsal shagreen . . . . . *D. septemmaculatus* (Becker)
Anal lobe without dorsal shagreen 5

5. Posterior portion of shagreen area on T IV & V with distinctive adjoining area of fine spine bands (Fig. 39G) . . . . . *D. cumberlandensis* sp. nov.
Shagreen areas on T IV & V without such areas 6

6. T VIII with 5 lateral lamellar setae; shagreen area on T III with anterior rows of larger spinules (Fig. 41J) . . . . . *D. pelochloris* (Kieffer)
T VIII with 4 lateral lamellar setae; shagreen area on T III with shagreen spinules larger in middle portion of area (Fig. 38C) . . . . . *D. candidibasis* (Edwards)

Key to Known Larvae of Oriental-Australasian *Dicrotendipes*

1. Frontal apotome with a large anteromesal ovoid or subquadrate area (Figs. 40E, I; 41Q); frontal process absent 2
   Frontal apotome with small weak to strong frontal pit or process, or without markings (Figs. 7D, 38K, 41G, 42G). 5
2. 6th lateral tooth of mentum rounded and fused/appressed to 5th lateral tooth (Fig. 41N) . . . . . *D. pelochloris* (Kieffer)
   6th lateral tooth not rounded or fused/appressed to 5th lateral tooth 3
3. Median tooth of mentum broad (Fig. 40F); 29–37, 33 ventromental strial ridges. . . . . *D. cumberlandensis* sp. nov.
   Median tooth of mentum not broad (Figs. 40B, K); if relatively broad, then ventromental plates with about 40 strial ridges 4
4. Ventromental plate with 39–45, 42 strial ridges . . . . . *D. conjunctus* (Walker)
   Ventromental plate with about 28 strial ridges . . . . . *D. pseudoconjunctus* sp. nov.
5. Frontal apotome with long ventral frontal process (Fig. 7D) . . . . . *D. septemmaculatus* (Becker)
   Frontal apotome without frontal process; a weakly defined frontal pit may be present 6
6. Head capsule integument appears grainy at 400X; 1st and 2nd lateral teeth of mentum separate 7
   Head capsule integument not grainy at 400X; 2nd lateral teeth of mentum fused/appressed to 1st laterals 8
7. Ventromental plate with 35–40 strial ridges . . . . . *D. jonmartini* sp. nov.
   Ventromental plate with 28–30 strial ridges . . . . . *D. sarinae* sp. nov.
8. Median tooth of mentum sunken well below level of 1st lateral teeth (Fig. 38G); 38–40 ventromental strial ridges; frontal pit absent . . . . . *D. candidibasis* (Edwards)
   Median tooth at same level as 1st lateral teeth; 21–23 ventromental strial ridges; frontal apotome with weak frontal pit . . . . . *D. flexus* (Johannsen)

Dicrotendipes balciunasi sp. nov. (Fig. 28)

TYPE LOCALITY: Fogg Dam, NE of Humpty Doo, Northern Territory, Australia.

TYPE MATERIAL: **Holotype:** male, AUSTRALIA: Northern Territory: Fogg Dam, 15 km NE Humpty Doo, at UV light, 5-X-1982, leg. J.K. Balciunas & J. Gillett (JB). **Paratypes** (22): same data as holotype, 20 males (JB). Western Australia: De Grey River, 80 km NE Port Hedland, 27-28-XI-1984, leg. B. & M. Baehr, 1 male (ZS); Mary River, 115 km WSW Hall's Creek, sandy river bed with some restpools, 17-18-XI-1984, leg. B. & M. Baehr, 1 male (ZS). Holotype to be deposited in AN; paratypes in AN, BM, JE, and ZS.

DIAGNOSIS: The immaculate wings, somewhat pediform superior volsella and short, squat median volsella will distinguish this species. The female and immature stages are unknown.

ETYMOLOGY: I am happy to name this species for Dr. Joe Balciunas, who collected the majority of the type material.

MALE IMAGO (n = 5)

COLOR (slide mounted specimens). Head and body brown, with posterior portions of abdominal tergites V–VIII lighter; legs light brown, apical ¼ of femora and fore tibiae dark brown; fore metatarsus light brown at base, gradually darkening distally, tarsomeres dark brown; mid and hind tibiae light brown with dark brown apices, metatarsi light brown, tarsomere 2 light brown proximally, darker brown distally, remaining tarsomeres brown. Wing immaculate, clear; with light yellow-brown veins.

LENGTH (4). Total 3.08–3.98, 3.67 mm. Thorax 0.90–1.05, 0.97 mm. Abdomen 2.10–2.98, 2.70 mm.

HEAD. Setae: temporal 29–40, 33; clypeal 9–17, 13; cibarial 5–16, 11. Palpomere lengths: 40–57, 46; 43–54, 50; 103–135, 112; 150–183, 163; 215–273, 243. Frontal tubercles 5–14, 8 long, 5 wide (3). AR 1.87–2.19, 2.10.

THORAX. Scutal tubercle well developed; humeral pit with 2–5 small to medium tubercles or a bare spot on cuticle. Acrostichals 12–13 (2); dorsocentrals 17–27, 20; scutellars 6–12, 8; prealars 6–10, 8.

WING. Length 1.38–1.60, 1.47 mm; width 0.44–0.51, 0.47 mm. FCu slightly distal to or below RM. VR 0.83–0.95, 0.91. Setae: brachiolum 2; squama 7–11, 8; R 6–14, 10; R_1 0; R_{4+5} 2.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 8–16, 11 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	670–810, 721	610–750, 654	660–840, 717
ti	495–620, 535	565–700, 605	720–920, 717
ta_1	970–770 (2)	260–330, 289	470–620, 539 (4)
ta_2	355–450 (2)	150–190, 167	250–320, 275 (4)
ta_3	305–360 (2)	105–140, 120	220–275, 240 (4)
ta_4	220–280 (2)	60–90, 74	120–165, 136 (4)
ta_5	130–150 (2)	60–80, 68	80–100, 91 (4)
LR	1.56 (2)	0.45–0.50, 0.48	0.65–0.76, 0.70 (4)
BV	1.92–1.94 (2)	3.45–3.80, 3.62	2.61–2.85, 2.74 (4)
SV	1.47–1.51 (2)	4.17–4.63, 4.36	2.57–3.01, 2.77

ABDOMEN. Ventral accessory setae on S VI not apparent.

HYPOPYGIUM (Figs. 28A, B) with 0–3 medial setae. Gonostylus normal, slightly curved medially, with 4–6, 5 preapical setae. Superior volsella (Fig. 28C) length 43–65, 53; width 34–

48, 39; LWR 1.1–1.9, 1.4; pediform (somewhat triangular in deformed individuals) with 4–5 sensilla chaetica. A short, squat, membranous median volsella present dorsal to base of inferior volsella. Inferior volsella length 78–108, 89; simply clubbed, with 8–10 sensilla chaetica scattered on apex; with one well developed ventral preapical seta. Anal point bare dorsally, not deflexed; with 3–6, 4 dorsal basal setae and 6–8, 7 lateral basal setae.

REMARKS. A most unusual species for the genus; along with *D. lindae* sp. nov., *D. balciunasi* possesses a median volsella. Unfortunately, the immature stages of both species are unknown. I see no reason for establishing a new genus for this species and *lindae;* however, this may be necessary once the immature stages are found.

Dicrotendipes bilobatus Kieffer (Fig. 29)

Dicrotendipes bilobatus Kieffer, 1917:222.
nec *Chironomus* (*Dicrotendipes*) *conjunctus* Walker 1856: Freeman 1961a:695.

DIAGNOSIS: The immaculate wings, digitiform superior volsella and sharply deflexed anal point, which is not visible from a dorsal view, will distinguish this species. The female and immature stages are unknown.

MALE IMAGO (n = 3)

COLOR (pinned specimens). Head light brown, antennae darker; thorax light yellow-brown with red-brown vittae, scutellum light yellow-brown, postnotum dark red-brown; abdomen dark red-brown, distally lighter on T III-IV; fore femur stramineous, apex brown, remainder of leg brown, mid and hind legs stramineous, apex of tibiae brown, metatarsi stramineous with apices brown, remainder of legs brown. Wings immaculate, light dusky brown; veins light yellow-brown.

LENGTH. Total 4.52–4.76, 4.63 mm. Thorax 1.14–1.23, 1.19 mm. Abdomen 3.38–3.56, 3.45 mm.

HEAD. Setae: temporal 30–41, 34; clypeal 14–17, 16; cibarial 14–15, 14. Palpomere lengths (2): 52–62; 65–70; 175–182; 205; 290–295. Frontal tubercles 23–30, 26 long, 10–12, 11 wide. AR 2.38–2.51, 2.46.

THORAX. Scutal tubercle well developed; humeral pit with 3 large tubercles. Acrostichals 10–14, 12; dorsocentrals 15–19, 17; scutellars 9–13, 11; prealars 8–10, 9.

WING. Length 2.58–2.69, 2.62 mm; width 0.66–0.67, 0.67 mm. FCu slightly distal to or below RM. VR 0.90–0.97, 0.92. Setae: brachiolum 2; squama 6–11, 9; R 19–25, 22; R_1 12–19, 16; R_4+_5 24–33, 29.

LEGS. Foretarsal beard apparently absent. Palmate sensilla chaetica: 9–16, 12 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1230–1240, 1237	1075–1110, 1090	1155–1190, 1172
ti	780–800, 793	990–1000, 993	1310–1320, 1313
ta_1	1560–1660, 1617	560–590, 573	855–905, 873
ta_2	765–820 800	295–300, 298	430–465, 452
ta_3	610–660, 640	210–215, 212	350–355, 352
ta_4	475–510, 498	110–120, 117	180–190, 183
ta_5	200	90	110–115, 112
LR	2.00–2.08, 2.02	0.56–0.60, 0.58	0.65–0.69, 0.67
BV	1.68–1.75, 1.71	3.66–3.73, 3.71	3.01–3.15, 3.06
SV	1.23–1.29, 1.26	3.50–3.77, 3.64	2.74–2.92, 2.85

ABDOMEN. Ventral accessory setae on S VI not apparent.

HYPOPYGIUM (Figs. 29A, B) with 7–9, 8 medial setae. Gonostylus moderately wide, curved medially, with 5–6, 5 preapical setae. Superior volsella (Fig. 29C) length 80–95 (2); width 30–33 (2); LWR 2.7–2.9; digitiform with slightly expanded apex, with 6–8, 7 sensilla chaetica. Inferior volsella length 168–183 (2); with shallow apical notch, with 8–11 sensilla chaetica in 2–3 rows of 2–5 each; one well developed ventral preapical seta. Anal point narrow, bare dorsally, completely deflexed beneath T IX; with 0 dorsal basal setae and 9–10, 10 lateral basal setae.

REMARKS. Freeman (1961a) synonymized this species with *conjunctus* Walker on the basis of hypopygial similarities. Freeman apparently relied on Kieffer's figure (Kieffer 1917:Fig. 15) to do so. The hypopygium of *bilobatus* is unusual in that the anal point is strongly bent beneath T IX (Fig. 29); Kieffer's hypopygium figure does not show an anal point. I have seen pinned and fluid preserved specimens in which the anal point is strongly deflexed, and I assume that Kieffer had similar specimens before him. The superior volsellae of the 2 species are basically identical; the only character separating them is the anal point. Whether the strongly deflexed anal point is an artifact of preservation, a true species difference or perhaps an indication of a post-copulating condition may be resolved by examination of reared specimens. I am returning *bilobatus* to species status because of this uncertainty, with the hopes that it might interest workers to rear this unusual *Dicrotendipes*.

The type of *bilobatus* was apparently in the Hungarian National Museum and was probably lost in the fire of 1956 (Freeman 1961a).

MATERIAL EXAMINED: AUSTRALIA: Australian Capital Territory: Canberra, pond margin, 21 Nov. 1956, leg. W.W. Wirth, 1 male (US). New South Wales: Deewhy, South Creek, 27 Sept. 1956, leg. W.W. Wirth, 6 males (US).

Dicrotendipes candidibasis (Edwards) (Figs. 30, 38)

Chironomus (*Xenochironomus?*) *candidibasis* Edwards, 1924:573.
Chironomus melanocnemis Edwards, 1928:65. **NEW SYNONYMY.**

DIAGNOSIS: The adult is recognized by the distinctive wing and leg markings, the low number of acrostichal setae and the weakly sclerotized digitiform superior volsella of the male. The pupa can be separated by the 4 lateral lamellar setae on T VIII and the distinctive shagreen pattern. The unusual larva is recognized by its distinctive mentum with the sunken median tooth and the almost completely fused first and second lateral teeth.

MALE IMAGO (n = 5)

COLOR (pinned specimens). Head and thorax fuscous-light- brown, with scutellum lighter; abdominal T I-V with greenish base color, T II-IV with median brown saddle; T V with proximal ⅓ light green-brown, distal portion brown; T VI-VIII dark brown, hypopygium brown with gonocoxites, styli and volsellae white to very light brown; legs with femora greenish stramineous, fore and hind femora with brown apices; fore and hind tibiae with proximal 1/5 white, remainder brown or tibiae completely brown, mid tibia greenish-stramineous with light brown apex; fore metatarsus with extreme proximal light brown band followed by extensive white area and brown apical band, mid tibia with basal half white with postmedian brown band and white apex, hind tibia white with brown apex; all remaining tarsomeres brown. Wing with broad median band beginning at RM and extending distally through ⅓ to ½ of cells r_{4+5}, m_{1+2} and m_{3+4}; band stops at Cu_1 or continues to lower wing margin and extends forward or slightly proximal to FCu; also with dark areas over vannal fold and An.

LENGTH. Total 3.75–3.78 (2) mm. Thorax 1.05–1.08 (2) mm. Abdomen 2.65–2.85, 2.77 mm.

HEAD. Setae: temporal 16–32, 22; clypeal 20–39, 26; cibarial 8–10, 9. Palpomere lengths: 42–52, 47; 44–52, 50; 142–183, 166; 195–228, 209; 295–360, 318. Frontal tubercles 2 long, 5 wide (2). AR 1.43–1.73, 1.55.

THORAX. Scutal tubercle moderately developed; humeral pit well developed with many small to medium tubercles or 2 large tubercles or a pit. Acrostichals 0–2, 1; dorsocentrals 10–15, 12; scutellars 4–12, 7; prealars 6.

WING. Length 1.75–1.90, 1.84 mm; width 0.49–0.53, 0.51 mm. FCu below RM. VR 0.95–0.98, 0.96. Setae: brachiolum 1–2, 2; squama 2–6, 4; R 22–33, 27; R_1 10–17, 13; R_{4+5} 3–15, 2.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 8–16, 11 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1005–1170, 1057	790–950, 850	980–1180, 1051
ti	720–900, 774	660–800, 715	950–1120, 1013
ta_1	1130–1220, 1178 (4)	410–455, 439	630–690, 664
ta_2	555–610, 580 (4)	210–230, 218	330–410, 355
ta_3	460–500, 476 (4)	140	275–310, 290
ta_4	415–450, 430 (4)	55–60, 59	145–165, 151
ta_5	185–190, 188 (4)	50–60, 52	75–90, 83
LR	1.55–1.64, 1.59 (4)	0.56–0.64, 0.62	0.62–0.68, 0.66
BV	1.73–1.80, 1.76	4.00–4.63, 4.27	3.08–3.14, 3.10
SV	1.48–1.54, 1.50 (4)	3.44–3.89, 3.56	3.00–3.33, 2.51

ABDOMEN. 0–3 ventral accessory setae on S VI.

HYPOPYGIUM (Figs. 30A, B). Gonostylus normal, slightly curved medially, with 5–6 preapical setae. Superior volsella (Figs. 30C, D) length 20–43, 28; width 19–25, 24; LWR 0.8–2.3, 1.3; digitiform with membranous apex; with 4–6, 5 sensilla chaetica. Inferior volsella length 85–130, 104; notched slightly apically, with 1–5 sensilla chaetica in 1–3 rows, with 1–3 well developed ventral preapical setae. Anal point bare dorsally, not deflexed; with 1–6, 3 dorsal basal setae and 5–8, 7 lateral basal setae.

FEMALE IMAGO (n = 2)

COLOR. Similar to male. The band across the wing extends further distad in cell m_{1+2}.

LENGTH. Total 3.11 (1) mm. Thorax 1.16 (1) mm. Abdomen 1.95–2.03 mm.

HEAD. Setae: temporal 21–22; clypeal 34–36; cibarial 10–12. Palpomere lengths: 48–55, 43–50; 178–185; 210–245; 330–372. Frontal tubercles minute, not measurable. AR 0.46.

THORAX. Scutal tubercle moderately developed; humeral pit a well developed pit. Acrostichals 0–2 (3); dorsocentrals 16; scutellars 8–9; prealars 6.

WING. Length 2.08 mm; width 0.63–0.64 mm. FCu proximal to RM. VR 0.95–0.98. Setae: brachiolum 2; squama 7; R 30–36; R_1 15–16; R_{4+5} 31–33.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 36–42 on middle metatarsus; 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1100–1105	850–870	1030–1095
ti	760–790	710–750	980–1070
ta_1	1270–1310	455–470	660–680
ta_2	590–625	200–220	310–360
ta_3	510–520	135–140	275–295
ta_4	460–490	55	130–150
ta_5	200–205	55–60	80
LR	1.66–1.67	0.63–0.64	0.64–0.67
BV	1.74–1.78	4.40–4.53	3.21–3.36
SV	1.45–1.46	3.43–3.45	3.05–3.18

ABDOMEN. Ventral accessory setae not apparent on S VI. Notum 145–168; cerci 100–120. S VIII with 25–28 setae/side; X with 4–5 setae; Gc IX with 1–2 setae/side. ApL as in Fig. 30E.

PUPA: (n = 9)

COLOR. Clear with pale yellow-brown borders.

LENGTH. Total 4.13–4.79 (2) mm. Cephalothorax 1.00–1.13, 1.06 (3) mm. Abdomen 2.83–3.68, 3.23 (7) mm.

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 38A), 25–50 (2) high, 63–108 (2) wide. Dorsum moderately to well pebbled. Dc2 closer to Dc3. Thoracic horn base (Fig. 38B) with tracheal bundles fused.

ABDOMEN (Fig. 38C). Sternite I with very fine shagreen areas, S II-IV with fine lateral shagreen bands; S VI-VII with anterior pair of oval fine shagreen areas; T II with median broadly T-shaped shagreen area; T III-IV with median quadrilateral shagreen areas, areas narrower posteriorly; T VI with roughly V-shaped shagreen area; T VII with an anterior pair of suboval shagreen areas; T VIII with a pair of longitudinal bands of fine shagreen; shagreen areas on T II-VI with spines larger in middle portion of area. Tergites IV-V with posterior band of fine spinules. Posterior margin of T II with transverse row of 64–104, 89 hooklets. T VIII with 4 lateral setae. Caudolateral spurs on T VIII (Figs. 38D, E) single or with basal spurs. Anal lobes with 29–44, 37 setae. DR 1.84–2.23, 1.99.

FOURTH INSTAR LARVA: (n = 5)

COLOR. Head capsule light brown, postmentum darker.

HEAD. Postmentum length 238–250 (2). Mandible (Fig. 38F) length 188–210, 192, with 3 triangular lateral teeth; two well developed dorsal teeth present. Pecten mandibularis composed of 7–9, 8 setae. Mentum (Fig. 38G) with 13 teeth, median tooth sunk well below level of 1st laterals; 1st and 2nd lateral teeth fused, giving appearance of notched 1st lateral tooth; width 95–109, 103 (4); MR 2.24–2.48, 2.34 (4). Ventromental plate with smooth anterior margin; width 85–92, 88; length 47–54, 49. VPR 1.70–1.90, 1.78; IPD 49–56, 52 (4); PSR 1.64–1.78, 1.72 (4); 38–40, 39 strial ridges. Length of antennal segments (3): 38–40, 39; 51–60, 55; 17–19, 18; 8–10, 9; 7–8, 7. AR 1.02–1.15, 1.09 (3) (Fig. 38H). Inner blade of premandible (Fig. 38I) subequal to outer blade. Pecten epipharyngis (Fig. 38J) with 3 lobes. Anterior margin of frontal apotome (Fig. 38K) without discernible features, labral sclerite 1 smooth. S I with 6–9 fringes (Fig. 38L).

BODY. Ventral tubuli absent.

REMARKS. A large amount of reared material from Fiji differs from the holotype specimen of *D. candidibasis* only by the completely brown fore femora; in the holotype and one other specimen from Fiji the proximal portion of the fore femur is white. The superior volsellae of the specimens are similar; in the specimens with proximally white femora, the superior volsellae are slightly longer (Figs. 30C, D). Unless future reared material of specimens similar to the holotype is examined and shown to be radically different, I am considering all of these specimens to represent *D. candidibasis.*

I am here considering *Ch. melanocnemis* Edwards to be a junior synonym of *D. candidibasis.* I have seen a male from Samoa with genitalia similar to *candidibasis* but with leg color patterns as in *melanocnemis* (known only from the female). The foretibiae are unfortunately missing from this Samoan specimen. Leg color patterns (and other body coloration patterns) seem to be subject to considerable variation in other species of *Dicrotendipes,* and I do not consider them to be good specific characters.

It has been difficult to find morphological characters which will serve to separate females to species. The apodome lobe in the female genitalia may be of use in some instances. Apodome lobes of *candidibasis* and *melanocnemis* "types" are quite similar (Fig. 30E). In addition, in both males and females of both "types," the number of acrostichal setae is very low, or they are absent. I believe that *melanocnemis* is nothing more than a color variant of *candidibasis.*

Edwards (1924) described the hypopygium of *candidibasis* as lacking an anal point. I have mounted the holotype on a microscope slide (in balsam) and have observed that the anal point is contracted beneath T IX, somewhat similar to the anal point of *D. bilobatus.* I have also mounted the female holotype of *melanocnemis* in balsam on a microscope slide. Both types are in the BM.

MATERIAL EXAMINED: FIJI: Lautoka, 11-V-1921, W. Greenwood, 1 male (holotype *Ch. candidibasis*) (BM); Lautoka, 12-VI-1922, R. Veitch, 1 male (BM). Naduruloulou, at light, 8-X-1949, B.A. O'Conner, 5 females (det. *melanocnemis*) (BM); same locality & collector, 10-XI-1949, 1 female (det. *melanocnemis*) (BM). Viti Levu, Laucala Bay (Suva), 13-VI-1985, leg. J. Martin & C.J. Webb, 4 females (JM); Laucala Bay (Suva), egg mass #2, leg. J. Martin, 1 male/Pex/Lex, 2 males, 4 females, 1 pharate female pupa, 4 Pex (JM); Laucala Bay (Suva), egg mass #3, coll. from vegetation at edge of a stream (reared at 20° C), 13-VI-1985, leg. J. Martin, 1 male/Pex, 1 male, 2 pharate male pupae, 1 female/Pex, 2 females, 4 Pex, 2 Lex (JM); Laucala Bay (Suva), grounds of University of the South Pacific, egg mass #4, 13-VI-1985, leg. J. Martin, 7 males, 2 pharate male pupae/Lex, 10 females, 13 Pex, 2 larvae, 4 Lex (JM). SAMOA: Tutuila, Naval Station, at light, 29-VIII-1940, leg. Swezey & Zimmerman, 1 male (det. *melanocnemis*) (US). Upolu, Apia, II-1924, P.A. Buxton & G.H. Hopkins, 1 female (holotype *Ch. melanocnemis*) (BM); Upolu, Tapatapao, 1000 ft., at light, 22-VII-1940, leg. Swezey & Zimmerman, 1 female (US).

Dicrotendipes conjunctus (Walker) (Figs. 31, 39, 40)

nec *Chironomus conjunctus* Loew 1850, in Keilbach 1982:351 *(nomen nudum);* Spahr 1985:22.
Chironomus conjunctus Walker, 1856:425; Skuse 1889:253.
nec *Chironomus blandus* Skuse, 1889:238.
nec *Chironomus blandellus* Kieffer, 1906:16.
nec *Dicrotendipes bilobatus* Kieffer, 1917:222.
Orthocladius conjunctus (Walker): Kieffer 1917:228.
Chironomus (*Dicrotendipes*) *conjunctus* Walker: Freeman 1961a:695.

DIAGNOSIS: The adult male is recognized by the lack of a foretarsal beard, the relatively straight digitiform superior volsella, moderately broad inferior volsella and well developed acrostichal setae. The pupae of *conjunctus* and *pseudoconjunctus* may be inseparable, but in the limited material available to me, *conjunctus* pupae have fewer spines (14–20) on the posterior margin of T V than *pseudoconjunctus* (26–31); both species are distinguished from *cumberlandensis* by the presence of these spines (lacking in *cumberlandensis*). The larva is distinguished by the moderately broad median tooth of the mentum (broader in *cumberlandensis,* narrower in *pseudoconjunctus*) and high strial ridge count (39–45, 42 in *conjunctus,* 29–37, 33 in *cumberlandensis*, 28 in *pseudoconjunctus*).

MALE IMAGO (n = 5)

COLOR (pinned specimens). Head greenish, pedicels light yellow-red-brown; thorax green with light red-brown vittae, scutellum green, postscutellum dark red-brown; abdomen brown with greenish tinge, T VIII and hypopygium brown or abdomen dark green with T VI-IX brown; fore femora green to greenish-stramineous, apices brown; tibiae and tarsi brown; mid and hind femora and tibiae greenish stramineous, metatarsi light brown, darkening apically, remaining tarsomeres brown. Wings immaculate, clear; with light brown veins.

LENGTH (4). Total 4.28–5.73, 4.78 mm. Thorax 1.18–1.58, 1.33 mm. Abdomen 3.10–4.15, 3.45 mm.

HEAD. Setae: temporal 37–53, 43; clypeal 18–25, 21; cibarial 13–16, 14. Palpomere lengths (4): 50–73, 56; 55–68, 61; 143–168, 154; 195–230, 206; 277–315, 293. Frontal tubercles 15–45, 32 long, 8–15, 10 wide. AR 2.28–2.74, 2.52 (4).

THORAX. Scutal tubercle moderately to well developed; humeral pit weak, scarlike or with 2–3 small tubercles. Acrostichals 7–17, 11; dorsocentrals 16–34, 21; scutellars 10–19, 13; prealars 10–11, 10.

WING. Length 2.18–2.68, 2.39 mm; width 0.60–0.75, 0.67 mm. FCu below RM. VR 0.94–0.96, 0.98. Setae: brachiolum 2–4, 3; squama 7–21, 12; R 22–28, 24; R_1 15–21, 18; R_{4+5} 18–30, 24.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 9–13, 11 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1005–1150, 1085	950–1040, 1003	1030–1170, 1106
ti	669–910, 788	850–1030, 932	1100–1370, 1224
ta_1	1305–1500, 1418 (4)	480–540, 509	755–900, 817
ta_2	590–720, 670 (4)	250–285, 264	380–480, 427
ta_3	490–580, 550 (4)	170–220, 190	300–405, 343
ta_4	410–490, 449 (4)	90–140, 109	155–230, 188
ta_5	180–220, 195 (4)	70–115, 91	95–140, 116
LR	1.65–2.08, 1.86 (4)	0.52–0.58, 0.55	0.65–0.69, 0.67
BV	1.67–1.85, 1.73 (4)	3.45–4.11, 3.76	2.79–3.09, 2.94
SV	1.24–1.38, 1.31 (4)	3.71–3.87, 3.80	2.79–2.95, 2.85

ABDOMEN. 1–3 ventral accessory setae on S VI.

HYPOPYGIUM (Fig. 31A) with 5–14, 8 medial setae, set within a weakly defined ovoid area. Gonostylus broad, curved medially, with 5–6 preapical setae. Superior volsella (Figs. 31B, C) length 68–100, 84; width 28–37, 30; LWR 2.5–3.2, 2.8; digitiform with short ventral extension (similar to that of *D. cumberlandensis,* cf. Fig. 32B); with 6–8, 7 sensilla chaetica. Inferior volsella length 145–175, 159; broad and notched slightly apically, with 1–6 sensilla chaetica in 1–4 rows, with 1–2 well developed ventral preapical setae. Anal point bare dorsally, slightly deflexed; with 0 dorsal basal setae and 7–12, 11 lateral basal setae.

FEMALE IMAGO (n = 2)

COLOR (pinned specimens). Head and thorax yellow-brown, with greenish tinge, scutellum green, postscutellum red-brown, abdominal T I-VI green, remainder brown; legs with femora greenish stramineous, tibiae light yellow-brown, metatarsi light yellow-brown proximally, becoming brown apically, remaining tarsomeres brown. Wing immaculate, clear; veins light brown.

LENGTH. Total 4.36 (1) mm. Thorax 1.43 (1) mm. Abdomen 2.93 (1) mm.

HEAD. Setae: temporal 33–38; clypeal 34–35; cibarial 15–17. Palpomere lengths: 50–58; 45–58; 148–172; 198–205; 320–338. Frontal tubercles 10–13 long, 8–9 wide. AR 0.43–0.44.

THORAX. Scutal tubercle well developed; humeral pit a scar with 2–3 tubercles. Acrostichals 14 (1); dorsocentrals 31–32; scutellars 17–20; prealars 8–12.

WING. Length 2.31–3.00 mm; width 0.79 (1) mm. FCu slightly distal to below RM. VR 0.90–0.93. Setae: brachiolum 2–3; squama 13–14; R 23–30; R_1 29–35; R_{4+5} 42–59.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 33–43 on middle metatarsus; 0–13 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1140	1000–1110	1170 (1)
ti	830–840	940–1050	1200–1440
ta_1	1390–1490	475–540	790–880
ta_2	610–680	240–270	370–450
ta_3	520 (1)	190	340–360
ta_4	450 (1)	110–120	170–190
ta_5	210 (1)	100–110	120–125
LR	1.67–1.77	0.51	0.61–0.66
BV	1.88 (1)	3.72–3.97	3.12 (1)
SV	1.33–1.42	4.00–4.08	2.97 (1)

ABDOMEN. 0–7 ventral accessory setae on S VI. Notum 205 (1); cerci 120–153. S VIII with 28–35 setae/side; X with 3–8 setae; Gc IX with 2–7 setae/side.

PUPA: (n = 3)

COLOR. Clear with pale yellow-brown borders.

LENGTH. Total 6.26 (1) mm. Cephalothorax 1.63 (1) mm. Abdomen 3.88–4.63 (2) mm.

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 39A), 55–70 (2) high, 33–45 (2) wide. Dorsum weakly to well pebbled. Dc_2 closer to Dc_3. Thoracic horn base (similar to *D. pseudoconjunctus,* Fig. 39J) with tracheal bundles narrowly joined to barely separated.

ABDOMEN (similar to *D. pseudoconjunctus,* Fig. 39K). Sternite I with very fine shagreen areas, S II-IV with scattered fine shagreen; S VI with anterior band of fine shagreen; T I with very sparse posterolateral shagreen areas; T II-V with median quadrilateral shagreen areas, with corners somewhat extended laterally; T VI with broadly V-shaped to hourglass-shaped shagreen area; T VII with an anterior pair of suboval shagreen areas; T VIII with an anterior and posterior pair of ovoid fine shagreen areas; shagreen areas on T II-V with spines larger in posterior portion of area, shagreen area on T VI with larger spines anteriorly and posteriorly; T II-IV with posterior area of fine spines. Posterior margin of T II with transverse row of 62–88, 73 hooklets; posterior margin of T V with 2 groups of 5–11 spines (14–20 total). A weak to strong reticulate cuticular pattern present on T IV (VI)-VIII. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Fig. 39B) 2–5, well developed, sinuate. Anal lobes with 45–73, 56 setae. DR 2.82–3.20, 3.13.

FOURTH INSTAR LARVA: (n = 4)

COLOR. Head capsule light brown to reddish yellow-brown, postmentum darker, postocciput dark-red to black.

HEAD. Postmentum length 247–378, 306. Mandible (Fig. 40A) length 208–298, 239 (3), with 3 triangular lateral teeth; two well developed dorsal teeth present. Pecten mandibularis composed of 14–16, 15 setae. Mentum (Fig. 40B) with 13 teeth, median tooth largest and higher than 1st lateral teeth; width 140–177, 164 (3); MR 2.33–2.45 (2). Ventromental plate with smooth anterior margin; width 125–150, 137; length 53–65, 59. VPR 2.31–2.36, 2.34; IPD 56–64 (2); PSR 2.34–2.64 (2); 39–45, 42 strial ridges. Length of antennal segments: 39–45, 42; 73–107, 91; 21–33, 27; 16–24, 21 (3); 7–8, 7 (3). AR 1.21–1.27, 1.24 (3) (Fig. 40H). Inner blade of premandible subequal to outer blade. Pecten epipharyngis (Fig. 40D) with 11–13, 12 lobes. Frontal apotome (Fig. 40E) with large anteromesal ovoid pit, labral sclerite 1 smooth. S I with about 16 fringes.

BODY. Ventral tubuli absent?

REMARKS. The first species belonging to *Dicrotendipes* described from Australia, *D. conjunctus* has been confused with several other species.

Kielbach (1982:351), in a list of amber insect fossils, records a "*Chironomus conjunctus* Loew, 1850." The name is a *nomen nudum,* for it is recorded only on the paper in which the amber specimen is wrapped; there is no publication with such a name (pers. comm., Odwin Hoffrichter to Jon Martin, 7 May 1984). Spahr (1985) also noted this situation, and listed "*Chironomus conjunctus*" as a "nomenklatorisch unverbindlicher Etikettenname" (nomenclaturally non-binding label-name).

Freeman (1961a) considered *Ch. blandellus* Kieffer (*nomen novum* for *Ch. blandus* Skuse, which was a junior objective primary homonym of *Ch. blandus* van der Wulp, 1858) a synonym of *conjunctus.* The only extant specimen is the female holotype. I have examined this specimen (housed in the AN) and conclude that it is not a *Dicrotendipes.* I have mounted the pinned specimen in balsam on a microscope slide. The specimen's ventrolateral lobe is very reduced, the apodome lobe is well developed with numerous microtrichia and the labia bear microtrichia; the species probably is a member of *Chironomus, Einfeldia* or another closely related genus.

Dicrotendipes bilobatus was also considered a synonym of *conjunctus* by Freeman (1961a); I am treating *bilobatus* here as a separate entity. See remarks under *D. bilobatus.*

Freeman (1961a) noted that more than 1 species may have been present in his *conjunctus* material. He found differences in the apical width of the inferior volsella and the extent of the foretarsal beard. He correctly stated that all existing names applied to specimens with broader appendages and no beard, i.e., *D. conjunctus.* Specimens with narrower inferior volsellae and a tarsal beard are *D. pseudoconjunctus.* At least a third similar species occurs with no tarsal beard and much broader (than *conjunctus*) inferior volsellae, *D. cumberlandensis* (q.v.).

In an unpublished Master's thesis, Martin (1961) briefly described the larva of *D. conjunctus* [as *Chironomus* (*Dicrotendipes*) *conjunctus* form C] with a "pair of quite long ventral tubuli on the penultimate segment." I have not examined any material of this species with such tubuli. Ventral tubuli are often present or absent on several other species of *Dicrotendipes* (Epler 1987a). Edward (1964) also described the larva and the pupa of *D. conjunctus.* He found the larvae inhabiting "algal mats and slime in permanent and temporary waters."

I have examined the type series of *conjunctus,* housed in the BM. It consists of a male and female, both pinned. The male bears the following labels: conjunctus n.s./VDL/Type; the female: VDL/68.4/Type. Because both specimens bear a type label, they must be considered syntypes. I hereby

designate the male as the lectotype and the female as a paralectotype for *Chironomus conjunctus* Walker. I have remounted both specimens in balsam on microscope slides.

MATERIAL EXAMINED: AUSTRALIA: Australian Capital Territory: Canberra, pond margin, 21 Nov 1956, leg. W.W. Wirth, 1 male (US). New South Wales: The Beardy Waters, nr Glenn Innes, 9-I-1968, leg. J. Martin, 1 male (JM); Boggy Swamp Creek on the Putty Road, 28-VIII-1981, leg. J. Martin, 2 males/Pex/Lex (JM); Deewhy, South Creek, 27 Sept 1956, leg. W.W. Wirth, 9 males (US, BM), same locality & collector, 23 Oct 1956, 3 males (US); Hornsby, at light, 6-8-I-1959, 1 male, 2 females [?] (BM). [Northern Territory]: V[an] D[ieman's] L[and], 1 male, 1 female (lectotype, paralectotype *Ch. conjunctus*) (BM). Tasmania: Advent Bay, 1 Jan 1922, leg. A. Tonnoir, 1 male (BM). Victoria: Botanic Gardens, Melbourne, 28-VIII-1963, leg. J. Martin, 1 male (JM); Chiltern, leg. J. Martin, 1 male (JM); Echuca, leg. J. Martin, 1 male (JM); Lorne, 5-III-1958, N. Dobrotworsky, 1 male (BM); Narbethong, 18-III-1958, N. Dobrotworsky, 3 males (BM); You Yangs, approx. 20 mls. SW Melbourne, 6-VII-1971, leg. J. Martin, 1 female/Pex/Lex (JM). No data, J. Martin, 1 Pex/Lex (JM).

Dicrotendipes cumberlandensis sp. nov. (Figs. 32, 39, 40)

TYPE LOCALITY: Cumberland River, 8 km S of Lorne, Victoria, Australia.

TYPE MATERIAL: **Holotype:** male/Pex/Lex, AUSTRALIA: Victoria: Cumberland River 8 km S of Lorne, 4-X-1967, leg. Jon Martin (JM). **Paratypes** (18): Queensland: Barron River, 100 m below Tinnaroo Dam Spillway, on *Hydrilla,* 18-X-1982, leg. J.K. Balciunas, 1 female/Pex (JB). Victoria: same data as holotype, 1 male/Pex/Lex, 1 female/Pex, 1 pharate female pupa/Lex, 2 larvae (JM); same data as holotype except 16-X-1967, 1 male, 1 female/Pex/Lex, 2 females/Pex, 1 female/Lex, 1 pharate female pupa/Lex, 6 larvae (JM). The holotype will be deposited in the AN; paratypes will be placed in BM, FS and JE.

ETYMOLOGY. This species is named for the Cumberland River, its type locality.

DIAGNOSIS: The adult male can be distinguished from the similar *D. conjunctus* and *D. pseudoconjunctus* by the massive inferior volsellae and by the absence of acrostichal setae. The female can be distinguished by the absence of acrostichal setae, which are replaced by setae-less pits. See diagnosis under *conjunctus* for pupae and larvae.

MALE IMAGO (n = 3)

COLOR (slide mounted specimens). Head, thorax and abdomen brown; fore femora light brown with darker distal apex, fore tibiae light brown with darker proximal and distal apices, mid and hind femora and tibiae light brown, all metatarsi light brown with darker apices, other tarsomeres brown. Wings immaculate with light brown veins.

LENGTH. Total 5.53–5.98 (2) mm. Thorax 1.48–1.50 (2) mm. Abdomen 3.18–4.48, 3.90 mm.

HEAD. Setae: temporal 35–43, 39; clypeal 14 (2); cibarial 17–19 (2). Palpomere lengths (2): 50–60; 73–95; 177–190; 225; 320–350. Frontal tubercles 18–22, 20 long, 6–8, 7 wide. AR 2.18–2.43, 2.30.

THORAX. Scutal tubercle moderately to well developed; humeral pit weak, scarlike or with 2–3 small tubercles. Acrostichals absent, 8–10 setae-less pits present; dorsocentrals 10–21, 16; scutellars 9–12, 11; prealars 9–10, 9.

WING. Length 2.38–2.93, 2.73 mm; width 0.67–0.79, 0.72 mm. FCu distal or below RM. VR 0.92–0.95, 0.94. Setae: brachiolum 2; squama 6–9, 7; R 27–28, 27; R_1 20–23, 21; R_{4+5} 27–38, 34.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 14–19, 16 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1115–1390, 1278	1040–1260, 1177	1110–1360, 1223
ti	780–1020, 907	915–1165, 1050	1150–1520, 1353
ta_1	1350–1870, 1590	540–680, 600	790–1030, 907
ta_2	570–790, 670	275–340, 298	390–500, 447
ta_3	475–620, 547	180–230, 202	275–380, 332
ta_4	380–480, 303	110–130, 118	140–190, 170
ta_5	180–195, 190	90–105, 100	115–130, 125
LR	1.68–1.83, 1.75	0.54–0.59, 0.57	0.65–0.69, 0.67
BV	2.02–2.07, 2.05	3.81–4.14, 3.94	3.17–3.32, 3.25
SV	1.29–1.45, 1.38	3.57–3.97, 3.72	2.80–2.88, 2.84

ABDOMEN. 0–1 ventral accessory setae on S VI.

HYPOPYGIUM (Figs. 32A, B) with 5–12, 8 medial setae, set within a weakly defined ovoid area. Gonostylus broad, curved medially, with 6–7 preapical setae. Superior volsella (Fig. 32C) length 93–95 (2); width 28–30 (2); LWR 3.2–3.3 (2); digitiform with short ventral extension, slightly curved mediad; with 9–10, 9 sensilla chaetica. Inferior volsella length 180–195 (2); apex extremely broad and notched slightly, with 1–7 sensilla chaetica in 2–3 rows, with 2–3 well developed ventral preapical setae. Anal point bare dorsally, slightly deflexed; with 0 dorsal basal setae and 13–20, 16 lateral basal setae.

FEMALE IMAGO (n = 3)

COLOR. Similar to male.

LENGTH. Total 3.80–5.53, 4.95 mm. Thorax 1.05–1.65, 1.44 mm. Abdomen 2.75–3.90, 3.51 mm.

HEAD. Setae: temporal 33–38, 36; clypeal 16–20, 18; cibarial 11–16, 14. Palpomere lengths: 58–75, 68; 55–80, 70; 138–190, 168; 167–247, 218, 173–385, 314. Frontal tubercles 3–15, 10 long, 7–8, 7 wide. AR 0.32–0.39, 0.36.

THORAX. Scutal tubercle well to moderately developed; humeral pit indiscernible. Acrostichals absent, 7–8 setae-less pits present; dorsocentrals 9–17, 14; scutellars 9–12, 11; prealars 8–10, 9.

WING. Length 2.70–3.53, 3.21 mm; width 0.84–1.09 (2) mm. FCu distal to RM. VR 0.86–0.89 (2). Setae: brachiolum 2–3, 2; squama 8–14, 11; R 21–31, 27; R_1 21–35, 29; R_{4+5} 48–52 (2).

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 25–27, 26 on middle metatarsus; 2–15, 6 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	1115–1510, 1375	1080–1390, 1283	1160–1470, 1357
ti	790–1090, 987	990–1240, 1152	1250–1630, 1490
ta_1	1550–2055, 1878	530–720, 647	810–1120, 993
ta_2	660–850, 763	260–350, 313	420–510, 474
ta_3	530–695, 623	180–245, 218	295–380, 348
ta_4	410–555, 495	110–140, 128	160–190, 180
ta_5	170–215, 193	100–120, 113	110–140, 127
LR	1.86–1.96, 1.91	0.54–0.58, 0.56	0.65–0.69, 0.67
BV	1.23–1.26, 1.24	3.91–4.06, 3.99	3.27–3.49, 3.40
SV	1.23–1.28, 1.26	3.64–3.91, 3.78	2.77–2.98, 2.88

ABDOMEN. 0–4 ventral accessory setae on S VI. Notum 170–245, 206 (4); cerci 110–180, 152. S VIII with 24–47, 36 setae/side; X with 1–10, 6 (4) setae; Gc IX with 0–1, 1 (4) setae/side.

PUPA: (n = 8)

COLOR. Light yellow-brown with darker borders.

LENGTH (5) Total 5.13–6.98, 6.23 mm. Cephalothorax 1.43–1.68, 1.57 mm. Abdomen 3.70–5.34, 4.66 mm.

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 39C), 53–58 (2) high, 100–133 (2) wide. Dorsum moderately to well pebbled. Dc_2 closer to Dc_3 (Fig. 39D). Thoracic horn base (Figs. 39E, F) with tracheal bundles narrowly joined to barely separated.

ABDOMEN (Fig. 39G). Sternites II-V with very fine shagreen areas; T II with broadly V-shaped median shagreen area with shagreen larger in posterior portion; T III-IV with median quadrilateral shagreen areas; T V-VI with somewhat lyrate shagreen areas; T VII with an anterior pair of suboval shagreen areas; T VIII with an anterior and posterior pair of ovoid fine shagreen areas; shagreen smallest in anterior portion of areas on T III-VI, subequal over rest of area; shagreen areas on T IV and V with distinctive adjoining area of fine spine bands

in posterior portion of area. Posterior margin of T II with transverse row of 63–92, 74 hooklets. A weak reticulate cuticular pattern present on posterior portion of T VII. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Figs. 39H, I) 1–3, well developed, sinuate, often with smaller basal spurs. Anal lobes with 39–82, 56 (7) setae. DR 2.48–3.38, 2.88 (7).

FOURTH INSTAR LARVA: (n = 5)

COLOR. Head capsule yellow-brown or reddish yellow-brown to brown, postmentum and genae darker, frontal apotome with darker borders on posterior ¾, labral sclerite 1 darker brown. Head capsule integument with grainy appearance.

HEAD. Postmentum length 240–320, 282 (3). Mandible length 253–265 (2), with 3 triangular lateral teeth; two dorsal teeth present. Pecten mandibularis composed of 10–15, 12 (3) setae. Mentum (Fig. 40F) with 13 teeth, median tooth broadly rounded; width 145–200, 173 (4); MR 2.67 (1). Ventromental plate with mostly smooth anterior margin; width 107–124, 115; length 53–70, 60. VPR 1.77–2.09, 1.94; IPD 65–89, 74 (4); PSR 1.39–1.69, 1.55 (4); 29–37, 33 strial ridges. Length of antennal segments (4): 62–88, 74; 18–20, 19; 12–13, 12; 15–19, 16; 7–8, 7. AR 1.13–1.60, 1.35 (Fig. 40G). Inner blade of premandible greater than outer blade. Pecten epipharyngis (Fig. 40H) with 3–6 (2) lobes. Frontal apotome (Fig. 40I) with large ventral anteromesal ovoid pit, labral sclerite 1 smooth, S I with 6–11, 9 (4) fringes.

BODY. Ventral tubuli absent.

REMARKS. A large species similar to *D. conjunctus, D. cumberlandensis* has distinctive large inferior volsellae and lacks acrostichal setae. In their place is a series of indentations; there is no trace of setae or their sockets.

The pupa lacks the hooklets usually found at the posterior margin of T V in pupae of this group.

Dicrotendipes flexus (Johannsen) (Fig. 41)

Chironomus (*Limnochironomus*) *flexus* Johannsen, 1932:530.
Limnotendipes flexus (Johannsen): Lenz 1937:6.
Dicrotendipes flexus (Johannsen): Sublette & Sublette 1973:403; Hashimoto et al. 1981:14; Sasa 1985:33.

DIAGNOSIS. The adult male strongly resembles *D. nervosus* (Staeger), but can be separated by the apparently disjunct distributions and fewer setae on R & R_1, (21–26 in *flexus*, over 35 in *nervosus*). The bizarre pupa is distinguished by the distinctive shagreen. The larva is separated by its distinctive mentum with the 1st and 2nd laterals almost completely fused.

See adult description in Johannsen (1932:530) and Hashimoto et al. (1981:14). The female is undescribed.

PUPA: (n = 2)

COLOR. Light yellow-brown to light brown.

LENGTH. Total about 4.20 (1) mm and larger. Cephalothorax about 1.20 (1) mm. Abdomen 3.00–4.20 mm.

CEPHALOTHORAX. Cephalic tubercles very small to essentially absent. Dorsum moderately to roughly pebbled. Dc_2 closer to Dc_1. Thoracic horn base (Fig. 41A) with tracheal bundles separated.

ABDOMEN. (Fig. 41B). Sternite I with well developed large shagreen spinules; S II-III with well developed lateral shagreen bands and median shagreen areas; S IV with median fine shagreen area and posterior area of well developed shagreen spinules; S V-VII with anterior shagreen areas, S VIII with anterior shagreen area and posterior area of well developed spinules; T II-VII with median quadrilateral shagreen areas, posterior shagreen spinules larger except on T V-VI where median group of large spines present immediately posterior to small median bare area; T VIII with broadly T-shaped shagreen area with posterior lateral extensions from arms of "T"; anal disc with well developed shagreen pattern on anterior ½; T II-VI with lateral longitudinal shagreen bands; T III (IV)-V with posterior band of very fine spinules. Posterior margin of T II with transverse row of 70–95 hooklets. T VIII with 4 lateral setae. Caudolateral spurs on T VIII (Fig. 41C) single, thorn-like. Anal lobes with 97–156 setae. DR 1.80 (1).

FOURTH INSTAR LARVA: (n = 3)

COLOR. Head capsule light yellow-brown; postmentum darker.

HEAD. Postmentum length 218–273, 243. Mandible length 168–185 (2), with 3 triangular lateral teeth; one dorsal tooth present. Pecten mandibularis composed of 8–10, 9 setae. Mentum (Fig. 41D) with 13 teeth, 2nd lateral teeth reduced and fused to 1st laterals, giving appearance of notched 1st lateral teeth; width 120–130, 126; MR 2.42–2.73 (2). Ventromental plate with shallow crenulations; width 82–105, 92; length 44-52, 48; VPR 1.74–2.02, 1.92; IPD 59–61 (2); PSR 0.75–0.85 (2); 21–23, 22 strial ridges. Length of antennal segments: 51–60, 55; 18–22, 20; 10–11, 11; 11–14, 12; 5–6, 5. AR 1.06–1.20, 1.14 (Fig. 41E). Inner blade of premandible greater than outer blade. Pecten epipharyngis (Fig. 41F) with 3 lobes. Frontal apotome (Fig. 41G) with small, poorly developed (or barely visible) anteromedian frontal pit; labral sclerite 1 smooth. S I with about 8–13 fringes.

BODY. Ventral tubuli absent.

REMARKS. The pupa of *flexus* is most unusual for a *Dicrotendipes*. No other species in the genus displays such heavy ventral shagreen and spination, and such extensive shagreen areas on T VII-VIII.

A holotype and paratype are present in the BM. Both specimens are in alcohol in microvials; their hypopygia are mounted on microscope slides. There are few data in the microvials or on the slides, but code numbers are with the specimens. These numbers correspond to the numbers given in Lenz (1937) in his material examined (Vorkommen) listed at the end of each species account. Johannsen (1932) also lists locality data, but does not give the year in which the specimens were collected. Johannsen's figure of *flexus* (Johannsen 1932:Fig. 18) is of the distorted, upside down paratype's hypopygium; the holotype mount is much better, and one wonders why the poorer specimen was illustrated.

MATERIAL EXAMINED: AUSTRALIA: Northern Territory: Berry Springs, 57 km S. of Darwin, on *Hydrilla,* 4-X-1982, leg. J.K. Balciunas, 1 pharate male pupa/Lex (JB); same collection data except at UV light, 1 male (JB). [INDONESIA]: [JAVA]: Ostjava, R. Bedali, Ufer, 15-X-1928, (L4), 1 male (holotype *Ch. flexus*) (BM); Ostjava, R. Bedali; *Lyngbya*-Zone

(2-6 m Tiefe) 22-XI-1928, leg. Thienemann, (L26), (ZS). Sumatra: N. Sumatra, Lake Toba, along NE shore Samosir Is., ½ km N of Simanindo, on *Potamogeton,* 12-IX-1981, leg. J.K. Balciunas, 1 larva (JB); Lake Toba at Tuk-Tuk, 8 km WSW of Prapat, at UV light, 6-VIII-1982, leg. J.K. Balciunas, 1 male (JB). Sudsumatra: Ranau-See, Oberflache, 21-I-1929, 1 male, (R4a), (paratype *Ch. flexus*) (BM); Heisse Quellen am Ranau-See, 40°, *Lyngbya*-Zone, 5-II-1929, leg. A. Thienemann, (R38), 1 pharate male pupa (ZS).

Dicrotendipes jobetus sp. nov. (Fig. 32)

TYPE LOCALITY: Katherine Gorge, Northern Territory, Australia.

TYPE MATERIAL: **Holotype:** male, AUSTRALIA: Northern Territory: Katherine Gorge, 15 km NE Katherine, open *Spinifex-Eucalyptus* woodland, 6-8-XI-1984, leg. B. & M. Baehr (ZS). **Paratype** (1): AUSTRALIA: W. Australia: Young River Station, outpost camp lake, 11-12-1959, leg. D.H. Edward, 1 male (BM). Holotype to be deposited in ZS; paratype in BM.

DIAGNOSIS: The adult male is distinguished by its distinctive superior volsella. The female and immature stages are unknown.

ETYMOLOGY. The name is an anagram constructed from the names of my parents, John and Betty Epler, for whom I am quite pleased to name this species.

MALE IMAGO (n = 2)

COLOR (pinned specimen). Head, thorax and abdomen brown. Forelegs light brown, distal ½ of femur darker, base of metatarsus lighter brown; mid and hind legs light brown, distal ½ of metatarsi and other tarsomeres darker brown. Wings immaculate, clear; with brown veins.

LENGTH. Total 3.23-4.75 mm. Thorax 0.88-1.35 mm. Abdomen 3.23-4.75 m.

HEAD. Setae: temporal 30-42; clypeal 15-21; cibarial 11-18. Palpomere lengths: 40-57; 50-75; 107-140; 145-183; 213-310. Frontal tubercles (1) 20 long, 7 wide. AR 2.11-2.53.

THORAX. Scutal tubercle well developed; humeral pit with 1-5 large tubercles. Acrostichals 7-13; dorsocentrals 13-24; scutellars 11-16; prealars 8-11.

WING. Length 1.45-2.25 mm; width 0.44-0.65 mm. FCu below to slightly distal to RM. VR 0.91-0.95. Setae: brachiolum 2; squama 6-9; R 8-17; R_1 0-1; R_{4+5} 2.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 5-10 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs, p. 131.

ABDOMEN. Flattened setae not apparent on S VI.

HYPOPYGIUM (Fig. 33A) with 4-5 medial setae. Gonostylus normal, slightly curved medially, with 4-6 preapical setae. Superior volsella (Fig. 33B) length 60-83; width 30-53; LWR 1.6-2.0; obovate, widest apically, with 12 sensilla chaetica. Inferior volsella length 108-175; apex slightly notched, with 4-5 sensilla chaetica in 2 rows, with 1 well developed ventral preapical setae. Anal point bare dorsally, slightly deflexed; with 6-8 lateral basal setae.

	P_1	P_2	P_3
fe	720–1010	620–910	670–965
ti	490–730	505–860	730–1100
ta_1	880 (1)	300–465	470–710
ta_2	430 (1)	150–240	250–375
ta_3	345 (1)	110–185	205–300
ta_4	270 (1)	70–120	110–175
ta_5	135 (1)	65-100	85–120
LR	1.80 (1)	0.54–0.59	0.64–0.65
BV	1.77 (1)	3.47–3.61	2.86–2.88
SV	1.38 (1)	3.75–3.81	2.91–2.98

Dicrotendipes jonmartini sp. nov. (Figs. 34, 42)

TYPE LOCALITY: Cook, South Australia.

TYPE MATERIAL: **Holotype:** male, [AUSTRALIA]: Cook, South Australia, from egg mass #1, [no date], leg. Jon Martin & B.T.O. Lee (JM). **Paratypes** (5): W. Australia: Shark Lake, Nth Esperance, 10-XII-1959, leg. D.H. Edward, 1 male (BM). Same data as holotype, 2 Pex, 2 larvae (JM). Holotype to be deposited in AN; paratypes in BM, AN, JE.

DIAGNOSIS: The adult male is distinguished by the pediform superior volsella and by its inferior volsella with its dorsal membranous extension. The female is unknown. The pupa is very similar to *D. sarinae* and may be inseparable; in the material available to me it is distinguished by the lower number of T II hooklets and higher number of spines on the posterior margin of T V. The larva possesses a granular head capsule integument and is distinguished from *D. sarinae* by the higher ventromental strial count and higher VPR and PSR.

ETYMOLOGY. I take great pleasure in naming this species for Dr. Jon Martin, who has been of immeasurable assistance during this study.

MALE IMAGO (n = 2)

COLOR (pinned specimen). Head, thorax, abdomen and legs brown. Wings immaculate; clear with light yellow-brown veins.

LENGTH. Total 4.03–4.65 mm. Thorax 1.15–1.25 mm. Abdomen 4.03–4.65 mm.

HEAD. Setae: temporal 31–43; clypeal 16; cibarial 15–19. Palpomere lengths: 50–53; 53–60; 128–135; 155–170; 277–293. Frontal tubercles 10–18 long, 9 wide. AR 2.55–2.66.

THORAX. Scutal tubercle well developed; humeral pit with 5–12 small to large tubercles. Acrostichals 11–13; dorsocentrals 20–27; scutellars 10–11; prealars 9–11.

WING. Length 1.70–2.00 mm; width 0.52–0.61 mm. FCu below to slightly proximal to RM. VR 0.98–1.00. Setae: brachiolum 2; squama 12 (1); R 11–12; R_1 0–2; R_{4+5} 2.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 7–14 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	790–845	760–780	840–890
ti	600–640	720–760	945–990
ta_1	940–980	330–360	640–650
ta_2	440–445	190–205	340
ta_3	395–400	155–170	290–300
ta_4	310	95–100	160
ta_5	160–165	80–85	110
LR	1.53–1.57	0.46–0.47	0.66–0.68
BV	1.78–1.87	3.39–3.48	2.69–2.78
SV	1.48–1.52	4.28–4.48	2.79–2.89

ABDOMEN. Flattened setae not apparent on S VI.

HYPOPYGIUM (Fig. 34A) with 7–15 dorsomedial setae. Gonostylus broad, almost straight medially, with 6 preapical setae. Superior volsella (Fig. 34B) length 58–63; width 43–47; LWR 1.2–1.5; pediform, with 5–6 sensilla chaetica. Inferior volsella with membranous dorsal extension, length 107–110; apex slightly notched, with 2–4 sensilla chaetica in 2–3 rows, with 4 well developed ventral preapical setae. Anal point bare dorsally, slightly deflexed; with 5–8 lateral basal setae.

PUPA: (n = 2)

COLOR. Mostly clear, cephalothorax light yellow-brown.

LENGTH. Total 4.68–4.83 mm. Cephalothorax 1.18–1.28 mm. Abdomen 3.50–3.55 mm.

CEPHALOTHORAX. Cephalic tubercles small. Dorsum moderately pebbled. Dc_2 closer to Dc_1. Thoracic horn base (Fig. 42A) with tracheal bundles narrowly joined.

ABDOMEN (Fig. 42B). Sternite I with weak anterolateral shagreen areas; S II-III with anterior and lateral fine shagreen areas; S VI-VIII with paired oval areas of fine shagreen; T I with weak anterolateral shagreen areas, T II with broadly T-shaped median shagreen area, T III-VI with median quadrilateral shagreen areas; T VII with anterior pair of ovoid shagreen areas; T VIII with anterior and posterior pairs of ovoid shagreen areas; shagreen on T III-VI larger medially. Posterior margin of T II with transverse row of 76–78 hooklets; T V with posterior continuous band of 42–44 spines. A weak reticulate cuticular pattern present on posterolateral portion of T VII. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Figs. 42C, D) 1–3, well developed, sinuate. Anal lobes with 31–33 setae. DR 2.11–4.50.

FOURTH INSTAR LARVA: (n = 2)

COLOR. Head capsule light brown with no postmental darkening. Head capsule integument with grainy appearance.

HEAD. Postmentum length 215 (1). Mandible length 188–190, with 3 triangular lateral teeth; 2 dorsal teeth present. Pecten mandibularis composed of 14–15 setae. Mentum (Fig. 42E) with 13 teeth, width 123–128; MR 2.86–3.00. Ventromental plate with smooth anterior margin; width 119–121; length 52–53; VPR 2.28–2.29; IPD 34–37; PSR 3.27–3.50; 35–40 strial ridges. Length of antennal segments (1): 69; 18; 13; 14; 7. AR 1.33 (1). (Fig. 42F). Inner blade of premandible greater than outer blade. Pecten epipharyngis with 3 lobes. Frontal apotome (Fig. 42G) with elongate-oval frontal pit, labral sclerite 1 smooth. S I with 8–9 fringes.

BODY. Ventral tubuli absent.

REMARKS. This species is very similar to *D. sarinae* in all life stages. It is possible that the *sarinae* material (all reared from 1 egg mass) may be aberrant *jonmartini.*

Dicrotendipes leei (Freeman)

Chironomus (*Dicrotendipes*) *leei* Freeman, 1961a:691.

See adult description in Freeman (1961a:691). The immature stages are unknown.

MATERIAL EXAMINED: AUSTRALIA: New South Wales: Hornsby, 6-I-1958, leg. D.J. Lee, 1 male (holotype) (SP); same data except 9-XII-1958, 1 male (paratype) (BM); same data except light trap, 7-II-1957, 1 female (without abdomen) (paratype) (SP); same data except 6-8-I-1959, (no collector data), 1 female (BM).

Dicrotendipes lindae sp. nov. (Fig. 35)

TYPE LOCALITY: Paradise River near Marion, Queensland, Australia.

TYPE MATERIAL: **Holotype:** male, AUSTRALIA: Queensland: Paradise River bei Marion, 25 km W Mackay, 22-12-1981, leg. M. Baehr (ZS). **Paratype** (1): AUSTRALIA: Northern Territory: 30 km N Adelaide River, tropical savannah woodland, 5-6-11-1984, leg. B. and M. Baehr, 1 male (ZS). Holotype and paratype in ZS.

DIAGNOSIS: The striking coloration of the body and wings, pediform superior volsella and long median volsella will distinguish this species. The female and immature stages are unknown.

ENTYMOLOGY. I take great pleasure in naming this beautiful species for my beautiful wife, Linda.

MALE IMAGO (n = 2)

COLOR (slide mounted specimens). Head, thorax and abdomen brown, abdominal T II-V with darker, narrow longitudinal band, wider on T VI and VII; posterior ⅓ of T VII and VIII lighter brown. Hypopygium brown, gonostyli and inferior volsellae white. Legs with all coxae dark brown; femora dark brown with light brown extreme distal and proximal apices and broad light brown median band; tibiae dark brown with light brown extreme proximal apices and median band; metatarsi light brown proximally, remainder of segment and following tarsomeres dark brown. The proximal dark brown band on the mid and hind tibiae is smaller than that on the fore tibia. Wings light dusky brown with darker clouds running from RM along R_{4+5} for approximately ¾ of its length, along Cu and in a band from the vannal fold to M_{3+4}, along and distal to AN, and along the alula; veins dark brown. The microtrichia within the dark clouds display a polygonal pattern at 100X.

LENGTH. Total 4.13–4.88 mm. Thorax 1.03–1.25 mm. Abdomen 3.10–3.63 mm.

HEAD. Setae: temporal 30–35; clypeal 18–19; cibarial 10 (1). Palpomere lengths: 48–55; 43–53; 137–180; 175–213; 243–297. Frontal tubercles 13 long, 10 wide. AR 2.13–2.38.

THORAX. Scutal tubercle well developed; humeral pit with about 8 small to large tubercles. Acrostichals 10–12; dorsocentrals 23–39; scutellars 11–16; prealars 9.

WING. Length 1.60–2.06 mm; width 0.45–0.62 mm. FCu slightly distal to or below RM. VR 0.92–0.96. Setae: brachiolum 2; squama 14; R 12–14; R_1 11–13; R_{4+5} 5–8.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 3–4 on middle metatarsus, 0 on hind metatarsus. Lengths and proportion of legs:

	P_1	P_2	P_3
fe	810–1050	760–915	840–1040
ti	610–775	665–870	895–1100
ta_1	1040–1350	350–460	610–720
ta_2	530–625	190–240	340–390
ta_3	410–510	115–170	270–305
ta_4	320–415	55–70	95–115
ta_5	160–190	60–70	90–95
LR	1.70–1.74	0.53	0.65–0.68
BV	1.73–1.82	4.08–4.23	2.95–3.16
SV	1.35–1.37	3.88–4.07	2.84–2.97

ABDOMEN. Flattened setae on S VI not apparent.

HYPOPYGIUM (Fig. 35A) with 16–18 dorsomedial setae. Gonostylus normal, slightly curved medially, with 4–7 preapical setae. Superior volsella (Fig. 35B) length 90–98; width 38–53; LWR 1.8–2.4; pediform, with 4 sensilla chaetica. A long thin membranous median volsella present laterad to base of superior volsella. Inferior volsella length 148–170; simply clubbed, with 4 sensilla chaetica in 2 rows; with 1 well developed ventral preapical seta. Anal point bare dorsally, deflexed; with 7–9 lateral basal setae.

Dicrotendipes pelochloris (Kieffer) (Figs. 36, 41, 50)

Tendipes pelochloris Kieffer, 1912:39; Kieffer 1916:113; Sublette & Sublette 1973:413 (listed as unplaced species of Chironomini).
Limnochironomus niveicauda Kieffer, 1921b:585. **NEW SYNONYMY.**
Chironomus (*Limnochironomus*) *niveicauda* (Kieffer): Johannsen 1932:528.
Chironomus inferior Johannsen, 1932:534. **NEW SYNONYMY.**
Cladotendipes inferior (Johannsen): Lenz 1937:7.
Chironomus (*Dicrotendipes*) *wirthi* Freeman, 1961a:692. **NEW SYNONYMY.**
Dicrotendipes inferior (Johannsen): Sublette & Sublette 1973:403.
Dicrotendipes niveicauda (Kieffer): Sublette & Sublette 1973:404; Hashimoto et al. 1981:13.
Kimius hoonsooi Ree, 1981:218; Sasa & Hasegawa 1983:321. **NEW SYNONYMY.**
Dicrotendipes niveicaudus (Kieffer): Sasa & Hasegawa 1983:321.
Xenochironomus loripes Guha et Chaudhuri, 1981:163. **NEW SYNONYMY.**
Einfeldia loripes (Guha et Chaudhuri): Chaudhuri & Guha 1987:27. **NEW SYNONYMY.**

DIAGNOSIS: The adult male is distinguished by the distinctive hypopygium with its sharply deflexed anal point and distinctive superior volsella. The female can usually be identified by its color pattern, and by the distinctive apodome lobe with well developed microtrichia. The pupa is separated by the shagreen pattern and 5 lateral lamellar setae on T VIII (see key); the larva can be separated by its distinctive mentum.

MALE IMAGO (n = 7)

COLOR (slide and alcohol specimens). Head and thorax brown to dark brown, abdominal T I-V yellow-green to green to dark brown, T VI-IX dark brown, gonostyli white to light brown. Legs with coxae yellow-white, femora with proximal 1/8–1/2 yellowish-white to white, distal portion dark brown; tibiae dark brown; fore metatarsus with proximal ½–⅔ yellowish-white to white with distal portion dark brown or complete metatarsus dark brown, remaining fore tarsomeres light brown to brown; ta_1 and ta_2 of mid and hind legs yellowish-white to white with distal apices brown, remaining tarsomeres brown, occasionally lighter proximally. Wings hyaline to dusky brown, some specimens with diffuse brown cloud along R_1, R_{4+5}, M, Cu and An; veins brown.

LENGTH. Total 3.74–4.40, 4.01 (4) mm. Thorax 1.06–1.25, 1.14 (4) mm. Abdomen 2.65–3.48, 2.99 (6) mm.

HEAD. Setae: temporal 43–53, 49; clypeal 11–23, 19; cibarial 8–12, 10. Palpomere lengths: 43–50, 47 (6); 47–63, 54 (6); 117–174, 140 (6); 158–195, 176 (5); 220–300, 265 (6). Frontal tubercles 16–26, 20 long, 7–10, 8 wide. AR 1.95–2.27, 2.09.

THORAX. Scutal tubercle moderately to well developed; humeral pit with 3–5 moderate tubercles. Acrostichals 9–14, 12; dorsocentrals 15–17, 16; scutellars 6–10, 8; prealars 7–10, 9.

WING. Length 1.73–2.28, 1.96 mm; width 0.51–0.67, 0.57 mm. FCu distal to RM. VR 0.81–0.92, 0.85. Setae: brachiolum 2–3, 2; squama 3–13, 7; R 14–25, 19; R_1 13–18, 15; R_{4+5} 18–24, 20.

LEGS. Foretarsal beard absent or very slight. Palmate sensilla chaetica: 11–18, 16 on middle metatarsus, 0–9, 4 on hind metatarsus. Lengths and proportions of legs (6):

	P_1	P_2	P_3
fe	885–1080, 962	850–1030, 913	970–1120, 1021
ti	610–770, 670	790–890, 795	940–1150, 1013
ta_1	1140–1280, 1247 (5)	370–475, 411	590–770, 654
ta_2	510–600, 556 (5)	180–260, 209	290–405, 339
ta_3	420–520, 462 (5)	130–170, 147	250–340, 286
ta_4	320–410, 357 (5)	55–80, 74	110–160, 143
ta_5	150–180, 167 (5)	55–80, 74	85–110, 102
LR	1.66–2.07, 1.86 (5)	0.49–0.54, 0.52	0.62–0.68, 0.64
BV	1.78–1.98, 1.89 (5)	4.06–4.74, 4.22	2.99–3.44, 3.10
SV	1.20–1.45, 1.33 (5)	3.98–4.38, 4.17	2.93–3.24, 3.12

ABDOMEN. 1–3 ventral accessory setae on S VI.

HYPOPYGIUM (Figs. 36A, B, C) with 10–16, 13 medial setae, apparently set within a weakly defined ovoid area. Gonostylus broad, curved slightly medially, with 6–9, 8 preapical setae. Superior volsella (Figs. 36D, E, F) length 65–77, 70 (6); width 31–40, 35 (6); LWR 1.8–2.2, 2.0 (6); somewhat digitiform, often with expanded apex directed mediad; with 2–4, 3 sensilla chaetica. Inferior volsella length 100–125, 111; apex simple, with 2–4 sensilla chaetica in 3–4 rows, with 2–4 well developed ventral preapical setae. Anal point bare, strongly deflexed so that it often is not visible dorsally; with 0 dorsal basal setae and 11–16, 13 lateral basal setae.

FEMALE IMAGO (n = 3)

COLOR. Generally similar to male, abdomen completely dark brown. Wings duskier than in male and in some specimens with a more distinct, darker cloud over R_1, R_{4+5}, M, Cu and An.

LENGTH. Total 3.16–4.11, 3.65 mm. Thorax 1.16–1.48, 1.32 mm. Abdomen 2.00–2.63, 2.32 mm.

HEAD. Setae: temporal 38–49, 43; clypeal 16–44, 29; cibarial 9–11, 10. Palpomere lengths: 47–55, 51; 48–60, 55; 118–180, 144; 162–193, 173; 223–300, 255. Frontal tubercles 5–13, 8 long, 5–8, 7 wide. AR 0.46–0.50, 0.48.

THORAX. Scutal tubercle well to moderately developed; humeral pit a low bare area to 5 small scattered tubercles. Acrostichals 10–12, 11; dorsocentrals 16–20, 18; scutellars 10–12, 11; prealars 8–10, 8.

WING. Length 1.97–2.75, 2.41 mm; width 0.67–0.88, 0.79 mm. FCu distal to RM. VR 0.83–0.91, 0.86. Setae: brachiolum 2–3, 2; squama 11–19, 16; R 19–23, 22; R_1 16–29, 23; R_{4+5} 28–41, 36.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 32–34, 33 on middle metatarsus; 12–23, 18 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	910–1130, 1043	860–1100, 995	970–1200, 1080
ti	600–850, 747	780–990, 897	950–1270, 1128
ta_1	1400–1585, 1465	375–510, 453	570–765, 688
ta_2	460–590, 528	180–240, 210	290–385, 343
ta_3	375–510, 445	130–165, 142	250–320, 287
ta_4	320–390, 357	75–80, 78	135–150, 142
ta_5	170–185, 177	75–80, 77	100–110, 105
LR	1.65–2.64, 2.02	0.48–0.52, 0.50	0.60–0.63, 0.61
BV	2.20–2.34, 2.17	4.33–4.94, 4.62	3.19–3.35, 3.30
SV	0.95–1.41, 1.23	4.09–4.37, 4.19	3.06–3.37, 3.22

ABDOMEN. 3–9 ventral accessory setae on S VI. Notum 182–215, 198; cerci 100–148, 132. S VIII with 21–26, 23 setae/side; X with 6–12, 9 setae; Gc IX with 2–4, 3 setae/side. DmL, VlL and ApL as in Fig. 25G; ApL with well developed microtrichia.

PUPA: (n = 7)

COLOR. Clear with yellow-brown margins; cephalothorax light brown.

LENGTH. Total 4.26–5.28, 4.67 (3) mm. Cephalothorax 1.10–1.25, 1.17 (3) mm. Abdomen 3.10–4.03, 3.54 mm.

CEPHALOTHORAX. Cephalic tubercles well developed (Fig. 41H), 63 (2) high, 75–88 (2) wide. Dorsum moderately to well pebbled. Dc_2 closer to Dc_1 or Dc_3. Thoracic horn base (Fig. 41I) with tracheal bundles joined or narrowly separated.

ABDOMEN (Fig. 41J). Sternite I with weak posterolateral shagreen, S II-IV with very fine scattered shagreen; S V-VII with weak anterior band of shagreen; T I sometimes with very weak anterolateral shagreen areas; T II with broadly V-shaped median shagreen area with shagreen slightly larger in anterior portion; T III-V with median quadrilateral shagreen areas, T III-IV shagreen areas with anterior band of well developed spines, T V shagreen with median area of stronger spines; T VII with an anterior pair of suboval shagreen areas; T VIII with an anterior and posterior pair of ovoid or elongate fine shagreen areas. Posterior margin of T II with transverse row of 64–90, 75 hooklets. A weak reticulate cuticular pattern present on posterior portions of T VII-VIII. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Figs. 41K, L, M) 1–4, small to well developed, often with smaller basal spurs. Anal lobes with 42–69, 59 (6) setae. DR 1.83–3.05, 2.46 (6).

FOURTH INSTAR LARVA: (n = 6)

COLOR. Head capsule light brown, postmentum slightly darker.

HEAD. Postmentum length 225–260, 243 (5). Mandible length 195–200, 197 (4), with 3 triangular lateral teeth, a depression proximal to 3rd tooth; two well developed dorsal teeth present. Pecten mandibularis composed of 8–9, 9 setae. Mentum (Fig. 41N) with 13 teeth, 6th lateral tooth broadly rounded, 5th reduced; width 123–153, 139 (5); MR 2.14–2.53, 2.39 (4). Ventromental plate with smooth anterior margin; width 85–106, 96; length 47–58, 53. VPR 1.73–1.88, 1.81; IPD 47–55, 51 (4); PSR 1.96–2.04, 2.01 (4); 30–34, 32 strial ridges. Length of antennal segments: 55–74, 67 (5); 20–33, 24 (5); 7–10, 9 (4); 11–13, 12 (4); 5–6, 6 (4). AR 0.90–1.51, 1.32 (4) (Fig. 41 O). Inner blade of premandible subequal to outer blade. Pecten epipharyngis (Fig. 41P) with 4–5, 5 lobes. Frontal apotome (Fig. 41Q) with large dorsal anteromesal ovoid depression, labral sclerite 1 smooth. S I with 6–8, 7 fringes.

BODY. Ventral tubuli absent.

REMARKS. A widespread species throughout the Oriental-Australasian areas. The distinctive hypopygium is very similar to that of the Afrotropical *D. kribiicola* (Kieffer); the immature stages of the 2 species differ sufficiently to maintain the 2 as separate species.

I have examined the type series of *Tendipes pelochloris,* housed in the IP. It consisted of 3 pinned specimens, apparently the 2 males and 1 female listed at the end of Kieffer's (1912) description. Because no holotype was designated, the 3 specimens must be considered syntypes. The specimens bear "type" labels that were obviously added at a later date (a viewpoint agreed to by Dr. H.J. Müller, director of the IP, in a personal communication, 23-III-1987). Two specimens bear "cotypus" and "paratypus" labels, the other specimen bears a "typus" and "holotypus" label. None of

these designations are valid, because holotypes and paratypes can only be fixed by the author in the original publication (International Code of Zoological Nomenclature, Chapter XVI (1985)).

I am designating as lectotype a male specimen, remounted on a microscope slide in Canada balsam, which bears the following labels: "LECTOTYPE, Tendipes pelochloris Kieffer, 1912/ J.H. Epler 1987/ Paratypus/ COTYPUS (with a line drawn through the word)/ Tainan, Formosa, H. Sauter, X, 08/ Coll. DEI, Eberswalde/ 87-1" (my personal identification number used in slide preparation) and my determination label. I have designated the other 2 specimens, a male and female, both still pinned, as paralectotypes. The male paralectotype consists only of a head (without antennae), thorax and a wing; it bears the following labels: "Tainan, Formosa, H. Sauter, X, 08/ Tendipes pelochloris (in Kieffer's handwriting)/ Holotypus/ TYPUS (with a line drawn through the word)/ Coll. DEI, Eberswalde/ PARALECTOTYPE" and my determination label. The female paralectotype bears similar labels with the exceptions of paratypus and COTYPUS (with a line drawn through the word) labels, and does not bear a Kieffer determination label. A non-type female specimen is also present in the IP collection. It bears a handwritten (in Kieffer's hand) label "*Cryptochironomus pelochloris* K." The specimen is a female *D. pelochloris* and has 3 ventral accessory setae on S VI. I have remounted this specimen in balsam on a microscope slide.

There is some variation in coloration. Specimens from Japan are strikingly marked, with females possessing wings with extensive smoky-brown "clouded" areas much darker than those of the male. Specimens from Thailand (not examined for this study) were apparently green (Hashimoto, et al. 1981). Many specimens examined from Australia, such as the type series of *wirthi,* are quite dark in general body coloration, and resemble the type series of *pelochloris.* I consider *wirthi* a junior synonym of *D. pelochloris;* the immature stages are morphologically inseparable.

The holotype of *Chironomus inferior* is a female specimen in alcohol with a wing mounted on a microscope slide. The specimen is bleached and lacks foretarsi. According to Johannsen (1932:535), this specimen was reared. Lenz (1937:7) described the larva and pupa of this species, but did not state that the specimens he described were the exuviae of the holotype, or how they were associated. I have examined a single larva and a female pupal exuviae determined by Lenz as *inferior.* All the specimens were apparently collected together (code #R38, see also Remarks under *D. flexus*). I am assuming that the immature stages are those of *inferior;* these immature specimens are inseparable from *D. pelochloris* and *inferior* becomes a junior synonym of *D. pelochloris.*

I've examined a larva, pupal exuviae and an adult male of *Xenochironomus loripes* Guha et Chaudhuri (determined as "*Einfeldia loripes*" by S.K. Das). Chaudhuri & Guha (1987) later placed this species in *Einfeldia*. I consider this species to be a junior synonym of *D. pelochloris*.

I was not able to locate a type specimen of *Limnochironomus niveicaudus*. It is not present in the collection at the University of the Philippines at Los Banos (V.J. Calilung, pers. comm.), the Hungarian National Museum (L. Papp, pers. comm.), the IP (H.J. Müller, pers. comm.) or the US (R.V. Peterson, pers. comm.).

This is 1 of 2 species known to me outside of the Neotropical region in which the male bears palmate sensilla chaetica on the metatarsus of the hind leg (the other species is *D. pseudoconjunctus*). These sensilla chaetica were present on all specimens examined except the males from Japan. They were present on all females examined, including those from Japan.

MATERIAL EXAMINED: AUSTRALIA: New South Wales, Mosman, light trap, 9 March 1957, leg. W.W. Wirth, 2 males (1 male holotype *wirthi* [US]; 1 male paratype *wirthi* [BM]); same data except 12-I-1957, 2 females (paratypes *wirthi* [US]). Northern Territory: Goanna Lagoon, Gulungil Creek, Alligator Rivers region, 3-XI-1979, leg. J. Martin, 1 male/Pex, 2 males (JM). Queensland: Sarina, egg mass Y, laid about 21-I-1969, leg. J. Martin & D.L. Porter, 4 males/Pex/Lex, 2 females/Pex/Lex, 1 pharate female pupa/Lex, 1 female (laid egg mass Y), 3 larvae (JM); Somerset Dam, ca. 80 ml. N. Brisbane, 25-V-1969, leg. J. Martin, 7 males, 1 female (JM). INDIA: Tamil Nadu: before Madurai, 25-IX-1985, leg. C.W. & L.B. O'Brien, 1 male (JE). West Bengal: Kalna, Sept. 1983, leg. S.K. Das, 1 male, 4 Pex, 1 larva (UB). [INDONESIA]: [Sumatra]: Sudsumatra, heisse Quellen am Ranau-See, 40°, *Lyngbya*-Zone, 5-II-1929, leg. A. Thienemann, 1 female (holotype *Ch. inferior*) (BM), 1 female Pex, 1 larva (ZS). JAPAN: Hamamatsu and Shizuoka, Aug-Nov 1984, H. Hashimoto, 6 males, 5 females (HH). PAKISTAN: Sind: Haleji Lake (Indus Delta), 23-VIII-1985, leg. C.W. & L.B. O'Brien, 3 males (JE). PHILIPPINES: Laguna Prov., Luzon, Laguna de Bay, Los Banos, 31-V-1983, leg. J.K. Balciunas, 2 males (JB). SOUTH KOREA: leg. H.I. Ree, 2 males (det. *K. hoonsooi*) (ZS). [TAIWAN] FORMOSA: Tainan, X-[19]08, H. Sauter, 2 males, 1 female (type series *pelochloris*); Taihoku, 7-IX-1912, H. Sauter, 1 female (det. "*Cryptochironomus pelochloris* K").

Dicrotendipes pseudoconjunctus sp. nov. (Figs. 31, 39, 40)

Chironomus (*Dicrotendipes*) *conjunctus* Walker. Freeman 1961a:695 (in part).

TYPE LOCALITY: Scotts Lagoon near Lady Barron, Flinders Island, Tasmania, Australia.

TYPE MATERIAL: **Holotype:** male/Pex/Lex. [AUSTRALIA: Tasmania]: Scotts Lagoon, near Lady Barron, Flinders Island, 11-II-1976, leg. Jon Martin & B.T.O. Lee (JM). **Paratypes** (13); AUSTRALIA: South Australia: Lake Leake, via Kalangadoo, from egg mass #4, [no date], leg. J. Martin, 1 male, 1 Pex (not associated with male) (JM). Tasmania: Arthurs Lakes, 28-I-1966, leg. G.F. Edmunds, 1 male (ZS); Interlaken, Lake Sorell, 14-X-1972, leg. J. Martin, 1 male (JM); Lake Leake, 21-X-1972, leg. J. Martin, 1 male (JM); Oatlands, Lake Dulverton, 12-II-1965, 2 males (JM). Victoria: Ocean Grove, 19-VIII-1960, leg. J. Martin, 1 male (BM);

same locality & collector, 16-XII-1960, 2 males (BM); South Melbourne, vicinity of Albert Park Lake, from egg mass A, laid-XII-1967, 2 males (JM). Western Australia: Lake Monger, 18-X-1956, D.H. Edward, 1 male (BM). The holotype will be deposited in the AN, paratypes in BM, JE, JM, ZS.

DIAGNOSIS: The adult male can be distinguished from the similar *D. conjunctus* and *D. cumberlandensis* by the strongly arched, medially directed superior volsella, by its smaller (than *cumberlandensis*) inferior volsella and by the presence of acrostichal setae. The female is unknown. See diagnosis for pupa and larva under *D. conjunctus*.

ETYMOLOGY: From the Greek *pseudos,* fallacy. Refers to the confusion of this species with the similar *D. conjunctus*.

MALE IMAGO (n = 5)

COLOR (pinned specimens). Head and thorax yellow-brown, scutellum pale green to green; abdomen green, T VI-VII darker, T VIII-IX brown. Legs light brown to brown, femora lighter on approximate proximal ½, tibiae sometimes lighter medially. Wings immaculate, very light dusky brown; veins brown.

LENGTH. Total 5.46–6.85 (2) mm. Thorax 1.37–1.75, 1.52 (3) mm. Abdomen 4.03–5.10, 4.45 (4) mm.

HEAD. Setae: temporal 45–49, 47; clypeal 17–22, 20; cibarial 8–18, 12. Palpomere lengths: 50–55, 53 (3); 55–75, 63 (4); 140–180, 163 (4); 188–215, 203 (4); 273–315, 285 (4). Frontal tubercles 23–33, 27 long, 8–13, 10 wide. AR 2.50–2.56, 2.52 (3).

THORAX. Scutal tubercle moderately to well developed; humeral pit weak, scarlike or with about 5 small tubercles. Acrostichals 8–18, 12 (4); dorsocentrals 18–36, 25; scutellars 11–19, 15; prealars 9–12, 10.

WING. Length 2.38–3.40, 2.75 mm; width 0.66–0.94, 0.78 mm. FCu slightly distal to or below RM. VR 0.91–0.96, 0.93. Setae: brachiolum 3–5, 4; squama 16–25, 21; R 16–24, 22; R_1 2–18, 11; R_{4+5} 11–24, 17.

LEGS. Foretarsal beard well developed. Palmate sensilla chaetica: 9–18, 13 on middle metatarsus, 0–5, 2 (4) on hind metatarsus. Lengths and proportions of legs (4), p. 141.

ABDOMEN. 0–1 ventral accessory setae on S VI.

HYPOPYGIUM (Fig. 31D) with 9–15, 11 medial setae, set within a weakly defined ovoid area. Gonostylus broad, curved medially, with 4–5, 5 preapical setae. Superior volsella (Fig. 31E) length 80–115, 96; width 33–43, 39; LWR 1.9–2.7, 2.5; somewhat digitiform with ventral extension, strongly curved mediad; with 7–13, 10 sensilla chaetica. Inferior volsella length 150–193, 167; apex broad and notched slightly, with 1–8 sensilla chaetica in 2–4 rows, with 2–5 well developed ventral preapical setae. Anal point bare dorsally, slightly deflexed; with 0 dorsal basal setae and 16–19, 18 lateral basal setae.

PUPA: (n = 2)

COLOR. Light yellow-brown with darker borders.

LENGTH. Total 5.60–6.08 mm. Cephalothorax 1.35–1.50 mm. Abdomen 4.25–4.58 mm.

CEPHALOTHORAX. Cephalic tubercles well developed, not measurable in specimens before me. Dorsum moderately pebbled. Dc_2 closer to Dc_1 or Dc_3. Thoracic horn base (Fig. 39J) with tracheal bundles narrowly joined.

ABDOMEN (Fig. 39K). Sternites I-IV with fine medio-lateral shagreen areas; S V-VIII with anterior pair of fine shagreen areas; T I with well developed reticulate cuticular pattern; T II with median quadrilateral shagreen area, shagreen larger in posteromedial portion, and weak

	P_1	P_2	P_3
fe	950–1200, 1035	950–1180, 1019	1015–1320, 1111
ti	770–1010, 840	900–1170, 980	1155–1500, 1259
ta_1	1190–1450, 1287 (3)	470–600, 515	750–950, 830
ta_2	535–650, 588 (3)	240–320, 271	410–510, 453
ta_3	470–570, 513 (3)	190–260, 215	320–410, 353
ta_4	390–470, 427 (3)	120–170, 136	175–230, 195
ta_5	170–225, 198 (3)	100–140, 113	110–155, 129
LR	1.44–1.58, 1.52 (3)	0.51–0.54, 0.53	0.63–0.69, 0.66
BV	1.75–1.91, 1.84 (3)	3.31–3.56, 3.43	2.73–2.89, 2.83
SV	1.44–1.52, 1.47 (3)	3.80–3.97, 3.88	2.73–2.97, 2.85

pair of anterolateral shagreen areas; T III with median quadrilateral shagreen area with anterolateral extensions, shagreen larger posteromedially; T II-III also with lateral longitudinal shagreen bands; T IV-VI with median quadrilateral shagreen areas, shagreen largest posterolaterally; T VII with anterior pair of suboval shagreen areas; T VIII with an anterior and posterior pair of ovoid fine shagreen areas; shagreen areas on T IV-V with distinctive adjoining area of fine spine bands in posterior portion of area. Posterior margin of T II with transverse row of 70–80 hooklets; posterior margin of T V with 2 groups of 12–17 spines (26–31 total). A well developed reticulate cuticular pattern present on T VII-VIII. T VIII with 5 lateral setae. Caudolateral spurs on T VIII (Fig. 39L) 1–3, well developed, sinuate, often with smaller basal spurs. Anal lobes with 46–66 setae. DR 3.18–3.76.

FOURTH INSTAR LARVA: (n = 1)

COLOR. Head capsule light brown, postmentum darker.

HEAD. Postmentum length 290. Mandible length 238, with 3 triangular lateral teeth; two well developed dorsal teeth present. Pecten mandibularis composed of 15 setae. Mentum (Fig. 40K) with 13 teeth; not measurable. Ventromental plate with smooth anterior margin; width 119; length 60; VPR 1.98; 28 strial ridges. Length of antennal segments: 90; 26; 14; 18; 6. AR 1.41. Inner blade of premandible greater than outer blade. Pecten epipharyngis with 3 lobes. Frontal apotome with large anteromesal ovoid pit, labral sclerite 1 smooth. S I with 13 fringes.

BODY. Ventral tubuli absent.

REMARKS. Freeman (1961a:695) first referred to this species as a possible new species in his discussion of *D. conjunctus*. He noted that some specimens had foretarsi with beards, and some variation in the inferior volsellae. Those specimens with bearded foretarsi were *D. pseudoconjunctus*.

The superior volsellae are markedly different (much more so than any differences in the breadth of the inferior volsellae noted by Freeman, although the inferior volsella of *pseudoconjunctus* is usually narrower apically than that of *conjunctus*) in the 2 species. The superior volsella in *D. pseudoconjunctus* is usually strongly arched mediad and has a more pronounced ventral apical extension (Fig. 31). The superior volsella of *D. cumberlandensis* is intermediate between that of *D. conjunctus* and *D. pseudoconjunctus;* however, *D. cumberlandensis* is easily distinguished by the huge apex to the inferior volsella and its lack of a foretarsal beard and acrostichal setae.

I can not reliably distinguish the pupa of *D. pseudoconjunctus* from that of *D. conjunctus.* The only difference noted between the 2 species was the number of spines at the posterior margin of T V; 14–20 spines in *D. conjunctus* and 26–31 in *D. pseudoconjunctus.* I have not found the number of these spines to be a reliable character in the other species of *Dicrotendipes* which possess them, but this does not preclude the possibility that these spines are a useful character in delimiting *D. conjunctus* and *pseudoconjunctus.* This might be tested by examining a larger series of specimens, for I was limited by an extremely small sample.

The same may be true for the larvae of these 2 species which I examined. I was able to examine only 1 larva of *D. pseudoconjunctus,* but it was markedly different from the larva of *D. conjunctus.* The *D. pseudoconjunctus* larva had a low ventromental plate strial ridge count (28) compared to *D. conjunctus* (39–45, mean 42).

I have also examined a male/Pex specimen from a pool near Lake Dove, Cradle Mt. Natl. Park, Tasmania, leg. J. Martin, 18-X-1972, which may belong here. The superior volsella resembles that of *D. pseudoconjunctus,* but the pupa would fit *D. conjunctus* utilizing the intersegmental hooklet counts discussed above. Most of the setae on the foretarsi have been lost and it is not possible to discern if the specimen possessed a foretarsal beard. The specimen may be an intermediate between *D. conjunctus* and *D. pseudoconjunctus,* and may indicate that *D. pseudoconjunctus* may be a higher latitude variant of *D. conjunctus.*

Dicrotendipes sarinae sp. nov. (Figs. 34, 42)

TYPE LOCALITY: Sarina, Queensland, Australia.

TYPE MATERIAL: **Holotype:** Male, AUSTRALIA: Queensland: Sarina, [ex] egg mass Z, laid about 21-I-1969, Jon Martin & D.L. Porter (JM). **Paratypes** (6): same locality & collectors, 19-I-1969, 1 female (laid egg mass Z) (JM); same data as holotype, 1 pharate male/Pex, 4 larvae (JM). Holotype to be deposited in AN; paratypes in AN, JE.

ETYMOLOGY. Named for the type locality.

DIAGNOSIS: The adult male can be distinguished from the similar *D. jonmartini* by the smaller, digitiform superior volsella. The pupa has more T II hooklets and fewer spines on the posterior margin of T V than *jonmartini*. The larva has fewer ventromental plate striae, higher VPR and lower PSR than *jonmartini*.

MALE IMAGO (n = 2)

COLOR (slide mounted specimens). Head, thorax, abdomen and legs brown. Wings immaculate, very light dusky brown; veins yellow-brown.

LENGTH (1). Total 4.23 mm. Thorax 1.08 mm. Abdomen 3.15 mm.

HEAD. Setae: temporal 35; clypeal 12–18; cibarial 7–10. Palpomere lengths (1): 52; 63; 108; 172; 243. Frontal tubercles 5–9 long, 8 wide. AR 2.18–2.37.

THORAX. Scutal tubercle moderately developed; humeral pit well developed with 11–12 well developed, large tubercles. Acrostichals 9–11; dorsocentrals 16–18; scutellars 9–12; prealars 5–7.

WING (1). Length 1.70 mm; width 0.57 mm. FCu below RM. VR 0.95. Setae: brachiolum 2; squama 7; R 6; R_1 0; R_4+_5 1.

LEGS. Foretarsal beard very sparse. Palmate sensilla chaetica: 9–10 on middle metatarsus, 0 on hind metatarsus. Lengths and proportions of legs (1):

	P_1	P_2	P_3
fe	770	720	790
ti	570	685	850
ta_1	920	310	590
ta_2	460	180	290
ta_3	375	140	275
ta_4	280	90	150
ta_5	145	70	100
LR	1.61	0.45	0.69
BV	1.79	3.57	2.74
SV	1.46	4.53	2.78

ABDOMEN. Ventral accessory setae not apparent on S VI.

HYPOPYGIUM (Fig. 34C) with 6–8 dorsomedial setae. Gonostylus broad, almost straight medially, with 4 preapical setae. Superior volsella (Fig. 34D) length 40–43; width 15–18; LWR 2.4–2.7; digitiform, slightly curved mediad; with 4–5 sensilla chaetica. Inferior volsella with membranous dorsal extension, with 1–3 sensilla chaetica on or near extension; length 75–100; apex clubbed, with 1–3 sensilla chaetica in 2 rows, with 2 well developed ventral preapical setae. Anal point bare dorsally, slightly deflexed; with 8–12 lateral basal setae.

FEMALE IMAGO (n = 1)

COLOR. Similar to male.

LENGTH. Total about 3.78 mm. Thorax 1.05 mm. Abdomen about 2.13 mm.

HEAD. Setae: temporal 34; clypeal 23; cibarial 13. Palpomere lengths: 55, 70; 135; 175; 260. Frontal tubercles 5 long, 8 wide. AR 0.46.

THORAX. Scutal tubercle well developed; humeral pit well developed with about 12 well developed tubercles. Acrostichals 7; dorsocentrals 25; scutellars 15; prealars 9.

WING. Length 1.56 mm; width 0.59 mm. FCu below RM. VR 0.87. Setae: brachiolum 2; squama 9; R 19; R_1 13; R_{4+5} 18.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 52 on middle metatarsus; 0 on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	779	710	770
ti	545	650	805
ta_1	870	300	530
ta_2	360	150	530
ta_3	305	100	—
ta_4	245	75	—
ta_5	135	70	80
LR	1.60	0.46	0.66
BV	2.09	4.20	—
SV	1.51	4.53	2.97

ABDOMEN. Ventral accessory setae not apparent on S VI. Notum 172; cerci 93. X with 10 setae; Gc IX with 1 seta/side.

PUPA: (n = 1)

COLOR. Light yellow-brown.

LENGTH. Not measurable.

CEPHALOTHORAX. Cephalic tubercles well developed, about 43 high, 75 wide. Dorsum moderately pebbled. Dc_2 closer to Dc_3. Thoracic horn base with tracheal bundles separated.

ABDOMEN. Damaged, but shagreen appears to be similar to *D. jonmartini* (Fig. 42B). Posterior margin of T II with transverse row of 95 hooklets. Posterior margin of T V with about 20 spines, apparently in single row. T VIII with 5 lateral setae. Caudolateral spurs on T VIII similar to *jonmartini* (Figs. 42C, D). Anal lobes with 32 setae. DR not measurable.

FOURTH INSTAR LARVA: (n = 3)

COLOR. Head capsule light brown, integument with grainy appearance.

HEAD. Postmentum length 193–205, 198. Mandible length 158–175, 165, with 3 triangular lateral teeth; two well developed dorsal teeth present. Pecten mandibularis composed of 9–10, 10 setae. Mentum (Fig. 42H) with 13 teeth; width 115–125; MR 2.88–2.98 (2). Ventromental plate with smooth anterior margin; width 85–92, 88 (4); length 47–50, 49; VPR 1.76–1.84, 1.80; IPD 35–41, 37; PSR 2.24–2.46, 2.38; 28–30, 29 (4) strial ridges. Length of antennal segments (4): 28–30, 29; 52–57, 55; 15–17, 16; 10–11, 10; 12–14, 13. AR 1.15–1.33 (Fig. 42I). Inner blade of premandible subequal to outer blade. Pecten epipharyngis with 3–4, 3 (4) lobes (Fig. 42J). Frontal apotome with weak elongate-oval frontal pit; labral sclerite 1 smooth. S I with 6–11, 8 fringes (Fig. 42K).

BODY. Ventral tubuli absent.

Dicrotendipes semiviridis (Kieffer)

Chironomus semiviridis Kieffer, 1911a:166; Johannsen 1932:532.
Dicrotendipes semiviridis (Kieffer): Sublette & Sublette 1973:404; Chaudhuri & Guha 1987:27.

I have seen only 1 specimen of this species, a female syntype from the Brunetti collection in the BM. The female (a pinned specimen) is a washed out yellow-green with no distinguishing marks; it appears to be a *Dicrotendipes.* There are no ventral accessory setae apparent on S VI.

Kieffer's figure (1911a:Fig. 24) and description contribute little to the identification of this species. According to Kieffer (1911a:111), the specimens he described in his 1911 paper were kept at the Indian Museum of Calcutta. These specimens are now apparently with the Zoological Survey of India, Calcutta. According to M. Datta, Zoological Survey of India (pers. comm., 12-XI-1986) specimens of *semiviridis* are in their collection, but "are in extremely miserable condition and are suggestive of not being mailed to anybody so as to save from further deterioration." Until the male of this species is redescribed (and because the female offers no specific characters), I consider *D. semiviridis* a *species inquirenda.*

MATERIAL EXAMINED: BURMA: Mandalay, 11-III-1908, N. Annandale, ex Brunetti coll., 1 female (syntype *semiviridis*) (BM).

Dicrotendipes septemmaculatus (Becker)

See description and remarks in Chapter II.

Dicrotendipes taylori (Freeman)

Chironomus (*Dicrotendipes*) *taylori* Freeman, 1961a:692.

See adult description in Freeman (1961a:692); the immature stages are unknown.

MATERIAL EXAMINED: AUSTRALIA: Queensland: Innisfail, [no date], F.H. Taylor, 2 males (holotype [SP]; paratype [BM]).

Dicrotendipes tenuiforceps (Kieffer) (Figs. 37, 51)

Tendipes tenuiforceps Kieffer, 1913a:136.
Chironomus (*Dicrotendipes*) *innisfailensis* Freeman, 1961a:694. **NEW SYNONYMY.**
Dicrotendipes tenuiforceps (Kieffer): Sublette & Sublette 1973:404; Chaudhuri & Guha 1987:27.

DIAGNOSIS: The adult male can be distinguished by its distinctive superior volsella. The immature stages are unknown.

MALE IMAGO (n = 2)

COLOR (pinned specimens). Head light brown, thorax golden yellow to orangish-yellow, abdomen yellow-orange to light green; legs greenish-stramineous, fore tibia light brown. Wings immaculate, clear; veins yellow-brown.

LENGTH. Total about 3.80 (1) mm. Thorax 0.78–1.10 mm. Abdomen about 2.70 mm.

HEAD. Setae: temporal 22–46; clypeal 10–16; cibarial 7. Palpomeres not measurable. Frontal tubercles 5–12 long, 5–7 wide. AR 2.03–2.33.

THORAX. Scutal tubercle well developed; humeral pit a scar or with 3–5 small tubercles. Acrostichals 6–12; dorsocentrals 11–12; scutellars 6–9; prealars 6–10.

WING. Length 1.48–1.63 mm; width 0.42–0.48 mm. FCu distal to RM. VR 0.85–0.86. Setae: brachiolum 2; squama 1–4; R 9–16; R_1 0–3; R_{4+5} 1.

LEGS. Foretarsal beard absent. Palmate sensilla chaetica: 5 (1) on middle metatarsus, 0 (1) on hind metatarsus. Lengths and proportions of legs:

	P_1	P_2	P_3
fe	730–920	590–750	700–870
ti	430–610	510–625	740–920
ta_1	910 (1)	285 (1)	470 (1)
ta_2	430 (1)	145 (1)	230 (1)
ta_3	395 (1)	90 (1)	200 (1)
ta_4	310 (1)	49 (1)	110 (1)
ta_5	145 (1)	45 (1)	60 (1)
LR	2.12 (1)	0.56 (1)	0.64 (1)
BV	1.62 (1)	4.33 (1)	3.18 (1)
SV	1.27 (1)	3.86 (1)	3.06 (1)

ABDOMEN. Flattened setae not apparent on S VI.

HYPOPYGIUM (Fig. 37A). Gonostylus thin, curved medially, with 5–7 preapical setae. Superior volsella (Fig. 37B) length 63–75; width 35–50; LWR 1.5–1.8; pediform-clubbed, apex directed laterad, with 5–8 sensilla chaetica. Inferior volsella length 112–115; apex simply clubbed; with 3–4 sensilla chaetica in 2 rows, with 1 well developed ventral preapical seta. Anal point bare dorsally, slightly deflexed; with 7 dorsal basal setae and 7–8 lateral basal setae.

REMARKS. Although not labeled as such, the single male specimen from the Brunetti collection in the BM may have type status. Kieffer's material for his 1913 paper was apparently kept at the Indian Museum of Calcutta and may now be with the Zoological Survey of India, Calcutta. I interpret a recent letter from M. Datta (with the Zoological Survey of India) as stating that no material of *tenuiforceps* is present in their collection. The Brunetti specimen was collected at Calcutta in September, which is in the range of dates Kieffer lists at the end of his description, and may be one of the original specimens described. Before any type status can be

inferred to this specimen, the collection at the Zoological Survey of India must be inspected in situ by a competent chironomid worker.

Freeman's *innisfailensis* (Freeman 1961a) is clearly a junior synonym of *tenuiforceps*, as evidenced by the distinctive hypopygium, and my examination of the holotype of *Ch. innisfailensis*.

MATERIAL EXAMINED: [AUSTRALIA]: Queensland: Innisfail, [no date], F.H. Taylor, 1 male (holotype *Ch. innisfailensis*) (SP). INDIA: Calcutta, 12-IX-1907, ex Brunetti coll., 1 male (BM).

FIG. 28. *D. balciunasi,* adult male. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Median and superior volsella, dorsal.

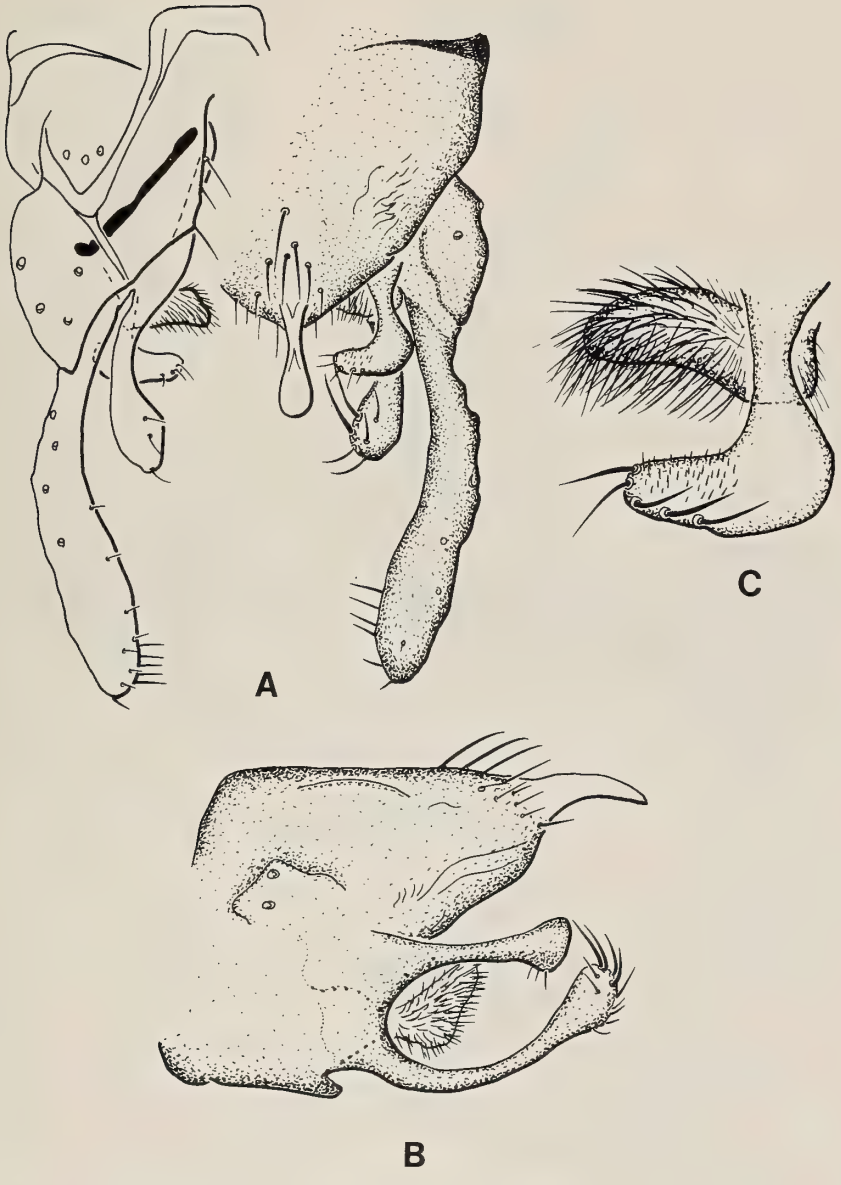

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FIG. 29. *D. bilobatus,* adult male. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, ventral.

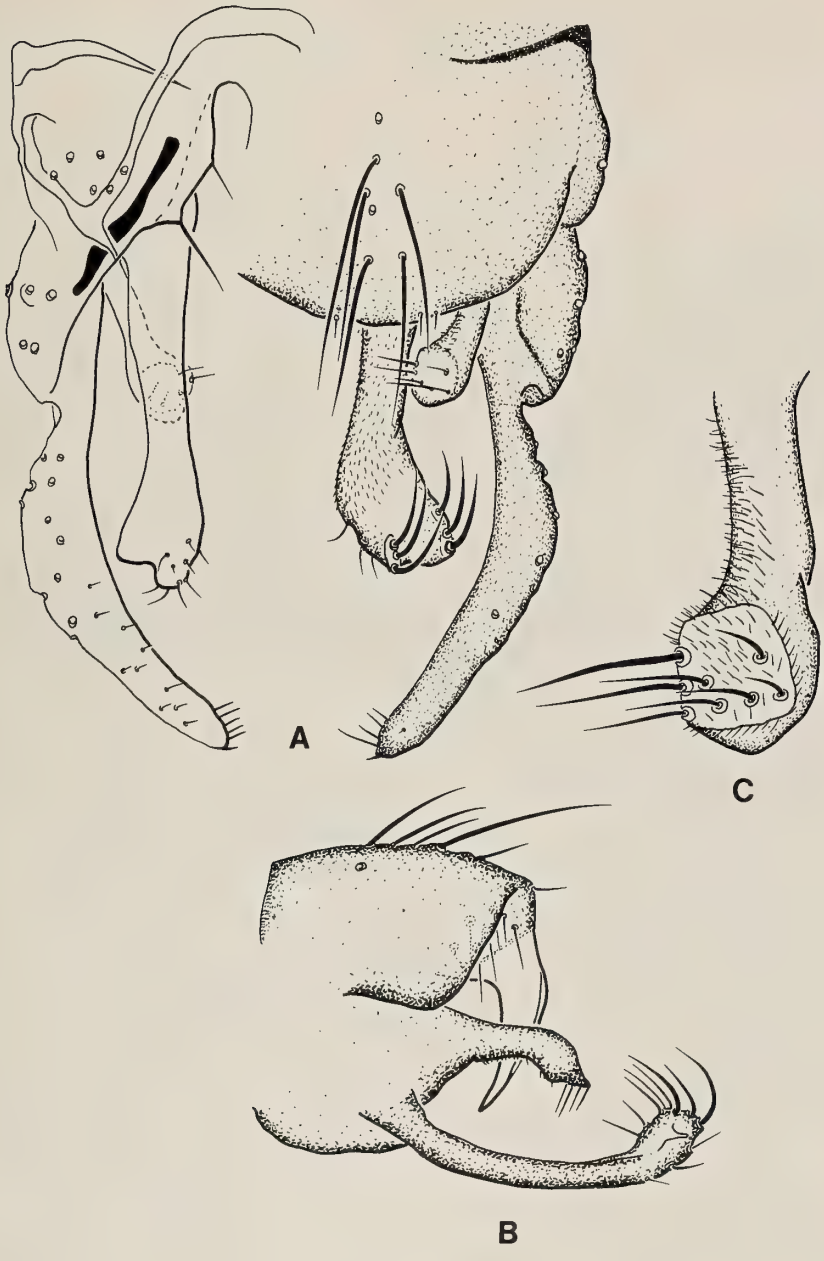
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FIG. 30. *D. candidibasis,* adult male and female. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, ventral. D) Superior volsella, ventral, holotype. E) Female ApL.

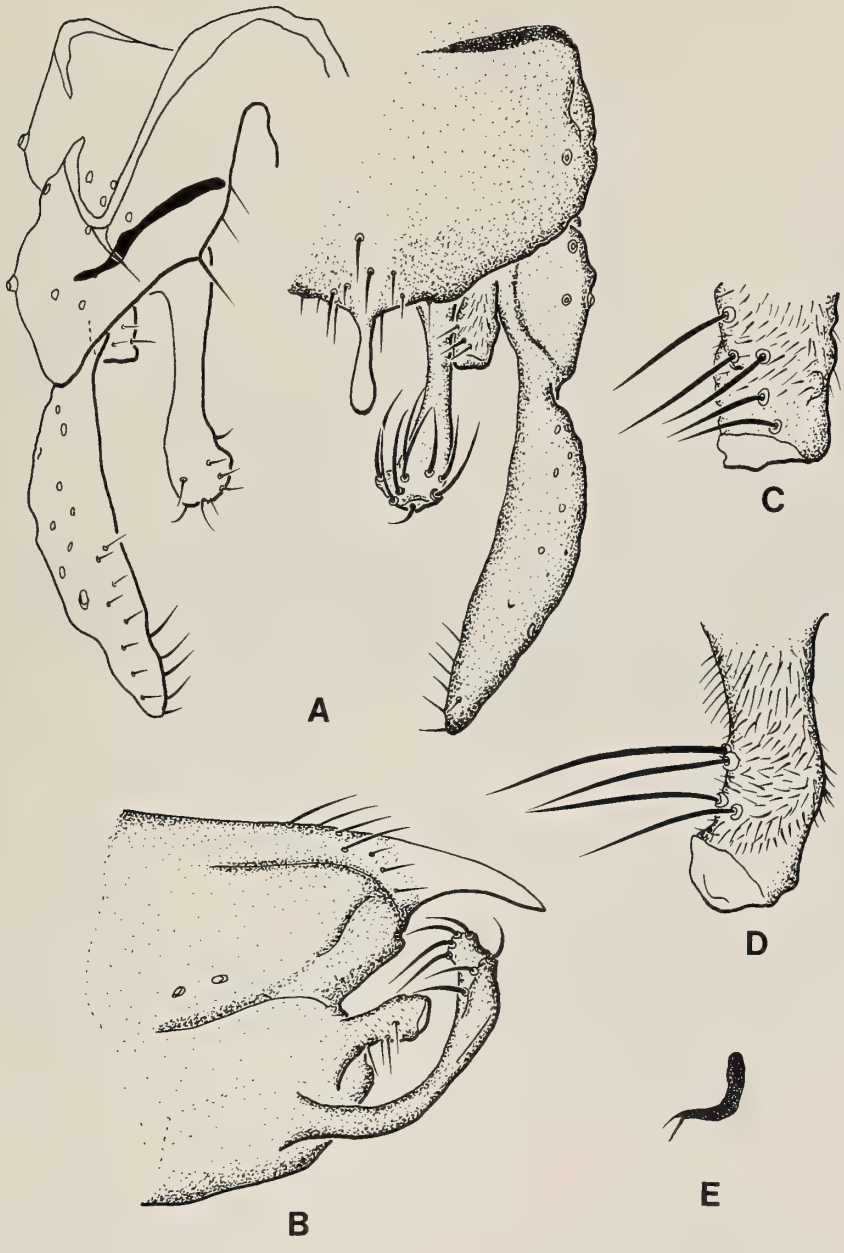
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FIG. 31. *D. conjunctus,* adult male (A-C). A) Hypopygium dorsal/ventral, lectotype. B) Superior volsella, ventral. C) Superior volsella, ventral, lectotype. *D. pseudoconjunctus,* adult male (D, E). D) Hypopygium, dorsal/ventral. E) Superior volsella, ventral.

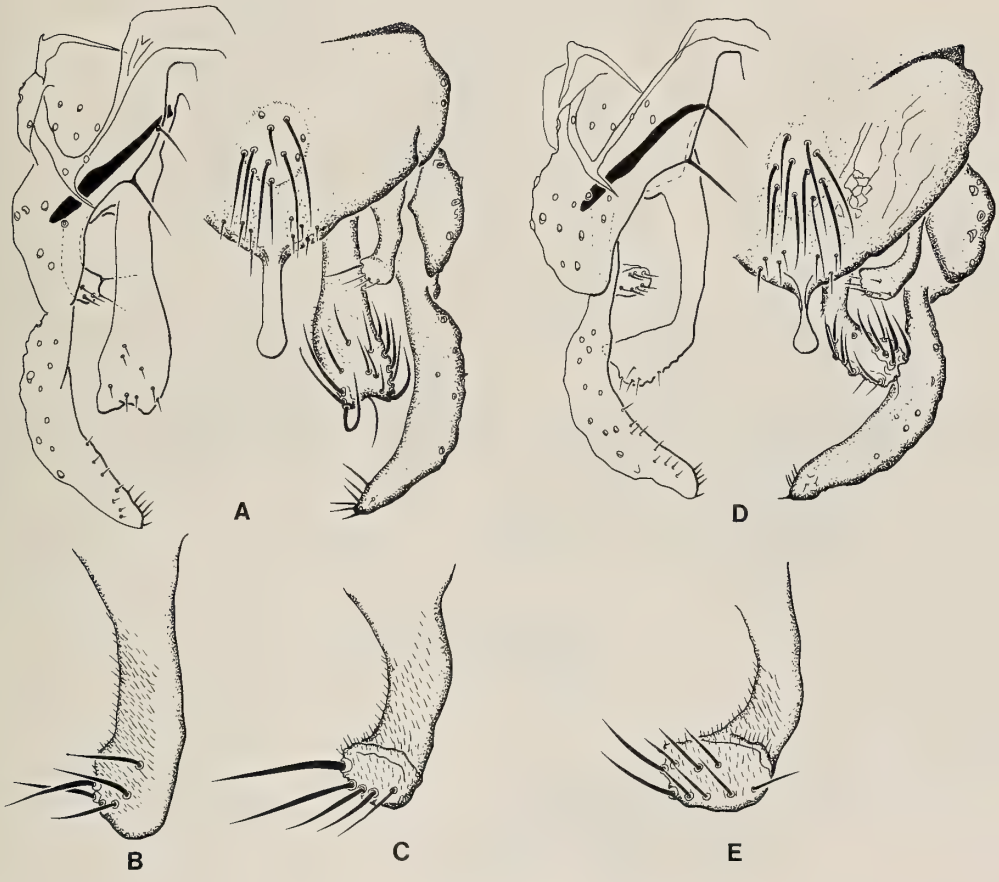
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FIG. 32. *D. cumberlandensis,* adult male. A) Hypopygium, dorsal/ventral. B) Hypopygium, lateral. C) Superior volsella, ventral.

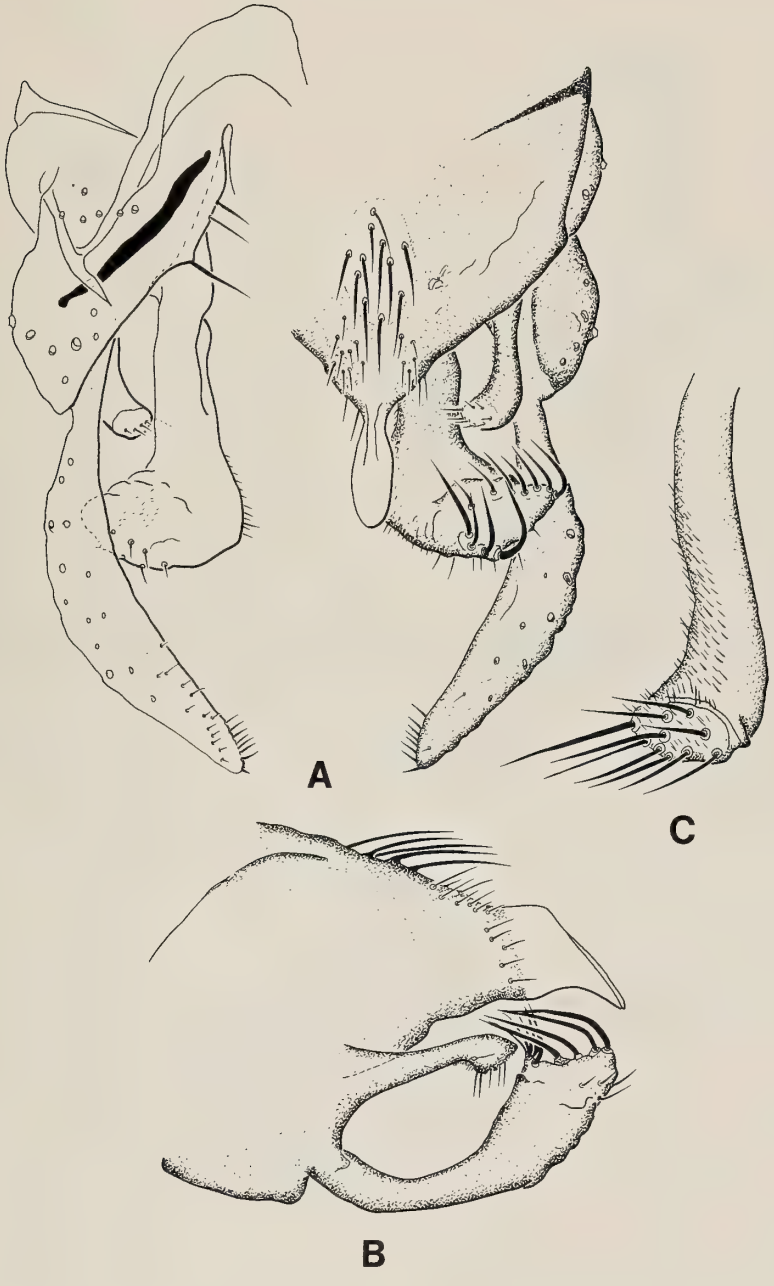
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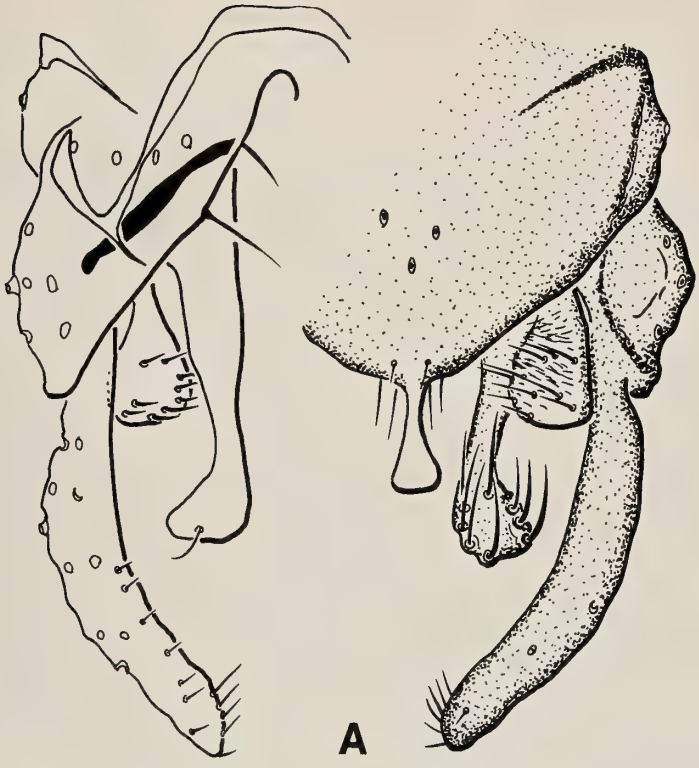
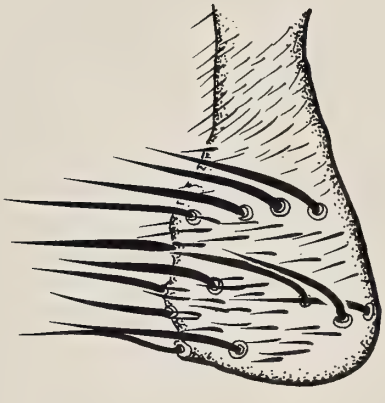
FIG. 33. *D. jobetus,* adult male. A) Hypopygium, dorsal/ventral. B) Superior volsella, ventral.



A



B

FIG. 34. *D. jonmartini,* adult male (A, B). A) Hypopygium, dorsal/ventral. B) Superior volsella, ventral. *D. sarinae,* adult male (C, D). C) Hypopygium, dorsal/ventral. D) Superior volsella, ventral.

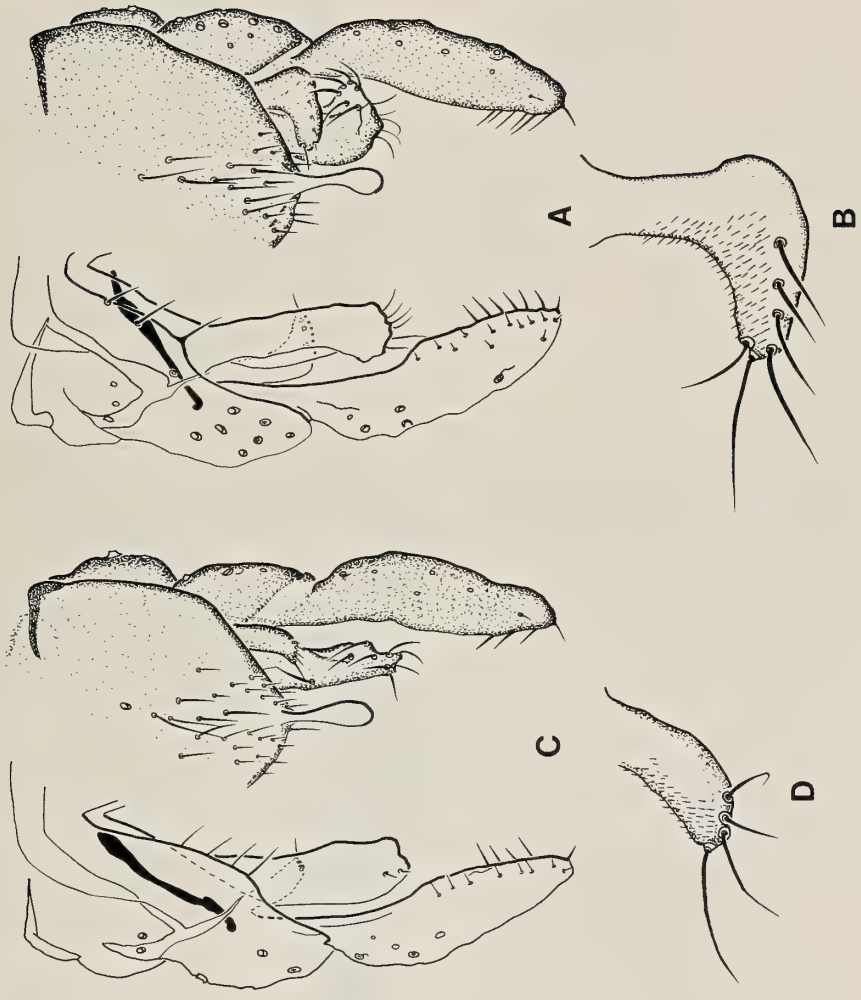

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FIG. 35. *D. lindae,* adult male. A) Hypopygium, dorsal/ventral. B) Median and superior volsella, ventral.

A

B

FIG. 36. *D. pelochloris,* adult male and female. A) Hypopygium, dorsal/ventral. B) Anal point variation. C) Anal point, lateral. D) Superior volsella, ventral, Australia. E) Superior volsella, ventral, Pakistan. F) Superior volsella, ventral, Japan. G) Female DmL, ApL, VlL.

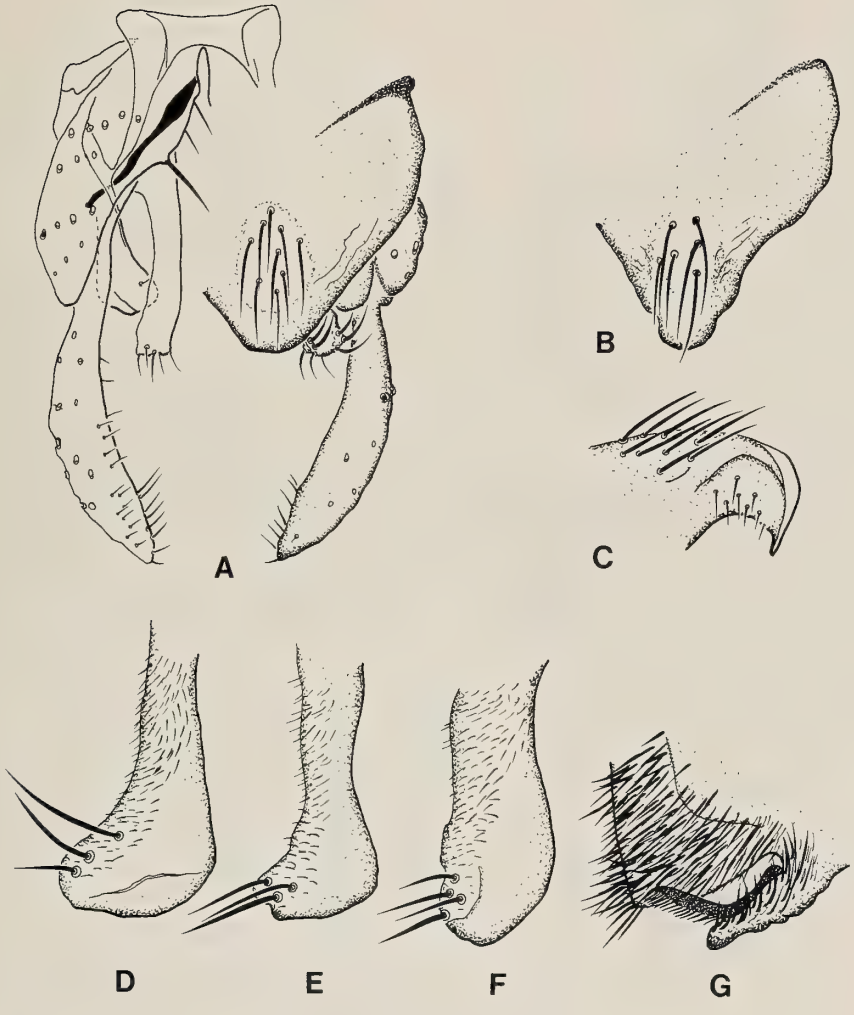
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FIG. 37. *D. tenuiforceps,* adult male. A) Hypopygium, dorsal/ventral. B) Superior volsella, ventral.

A

B

FIG. 38. *D. candidibasis,* pupa (A-E) and larva (F-L). A) Cephalic tubercle. B) Thoracic horn base. C) Abdomen, dorsal. D, E) Caudolateral spurs on T VIII. F) Mandible, ventral. G) Mentum and ventromental plate. H) Antenna. I) Premandible. J) Pecten epipharyngis. K) Anterior portion of frontal apotome and labral sclerites. L) SI.

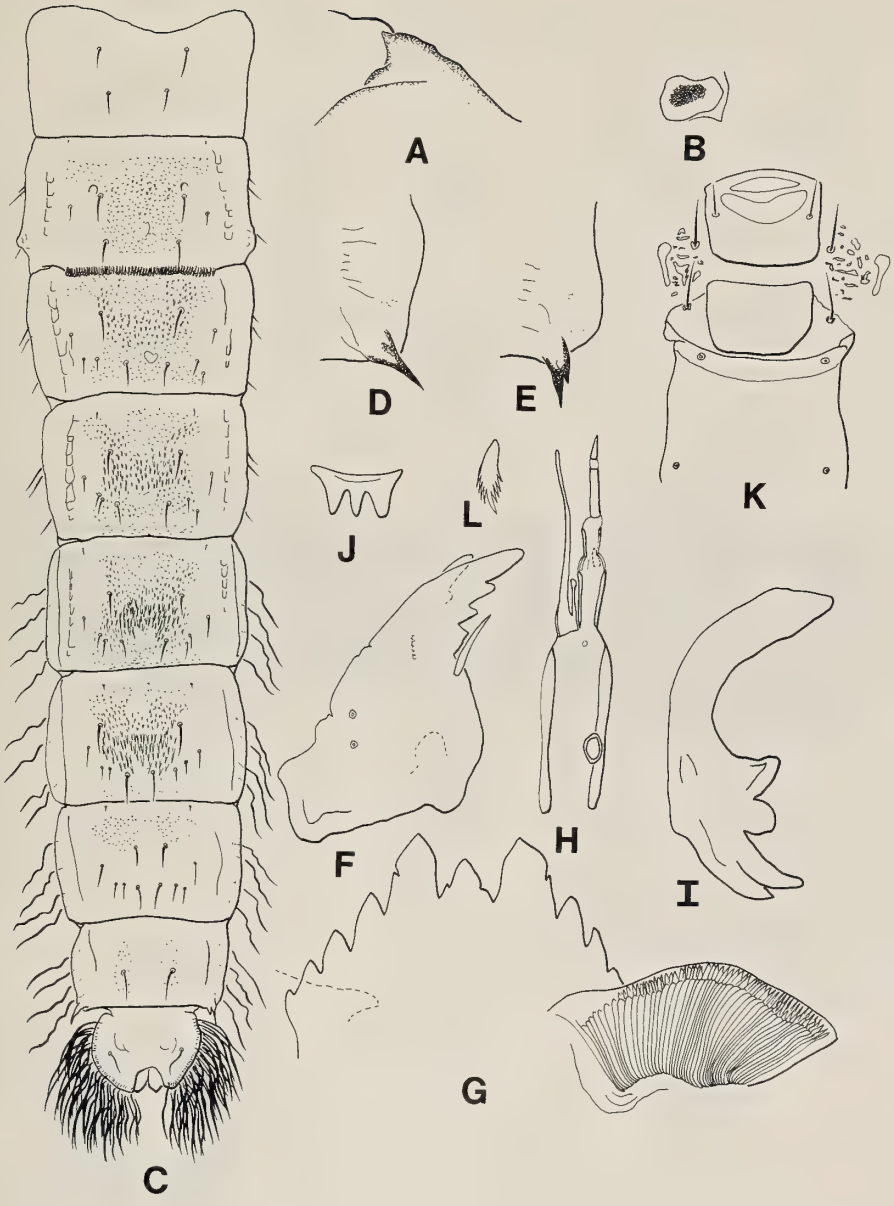
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FIG. 39. *D. conjunctus*, pupa (A, B). A) Cephalic tubercle. B) Caudolateral spurs on T VIII. *D. cumberlandensis,* pupa (C-I). C) Cephalic tubercle. D) Cephalothorax, lateral. E, F) Thoracic horn bases, showing variation. G) Abdominal tergites II-VIII, dorsal. H, I) Caudolateral spurs on T VIII. *D. pseudoconjunctus,* pupa (J-L). J) Thoracic horn base. K) Abdomen, dorsal. L) Caudolateral spurs on T VIII.

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FIG. 40. *D. conjunctus,* larva (A-E). A) Mandible, ventral. B) Mentum and ventromental plate. C) Antenna. D) Pecten epipharyngis. E) Anterior portion of frontal apotome and labral sclerites. *D. cumberlandensis,* larva (F-J). F) Mentum and ventromental plate. G) Antenna. H) Pecten epipharyngis. I) Anterior margin of frontal apotome and labral sclerites. J) SI. *D. pseudoconjunctus* larva. K) Mentum and ventromental plate.

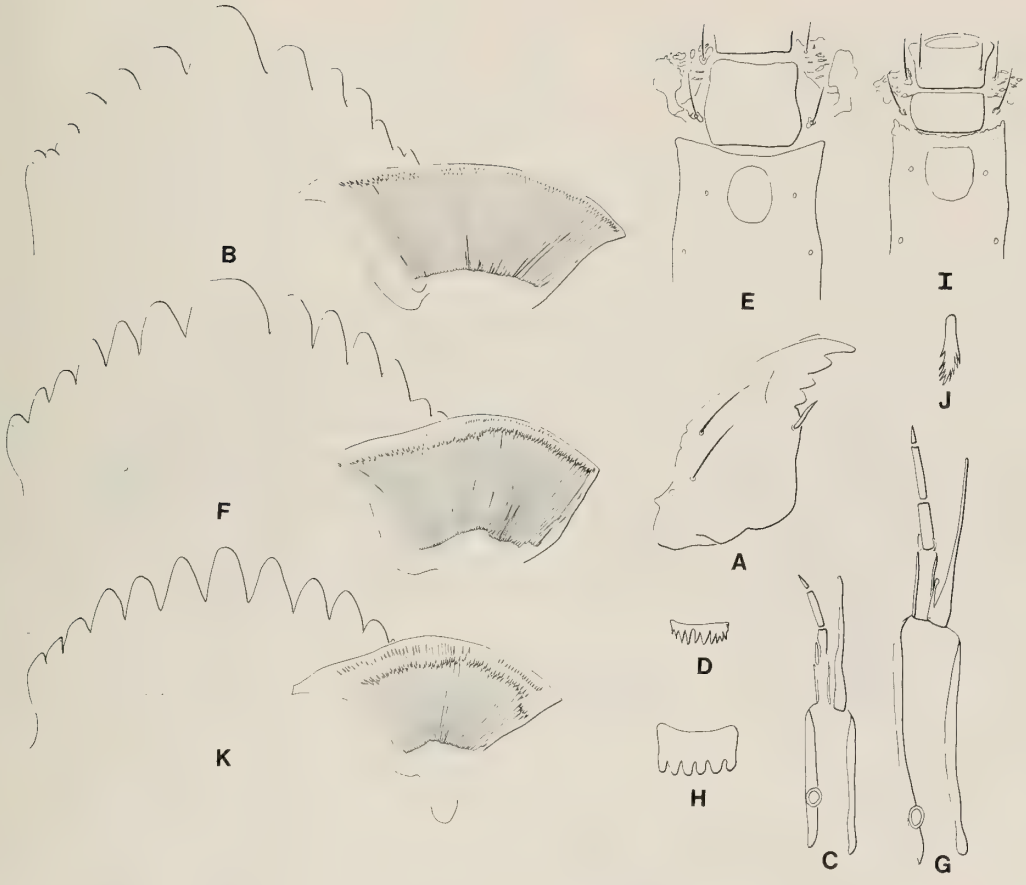
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FIG. 41. *D. flexus,* pupa (A–C) and larva (D-G). A) Thoracic horn base. B) Abdomen, dorsal. C) Caudolateral spur on T VIII. D) Mentum and ventromental plate. E) Antenna. F) Pecten epipharyngis. G) Anterior portion of frontal apotome and labral sclerites. *D. pelochloris,* pupa (H-M) and larva (N-Q). H) Cephalic tubercle. I) Thoracic horn base. J) Abdomen, dorsal. K-M) Caudolateral spurs on T VIII. N) Mentum and ventromental plate. O) Antenna. P) Pecten epipharyngis. Q) Anterior portion of frontal apotome and labral sclerites.

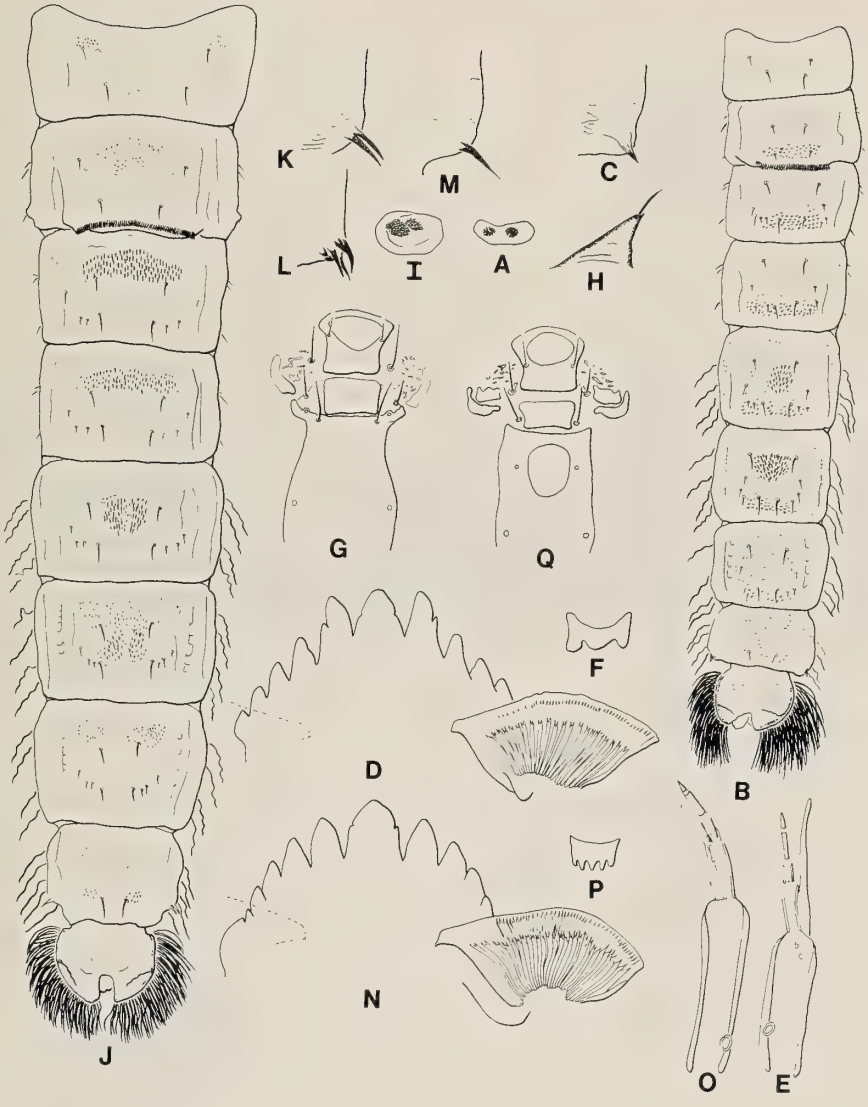
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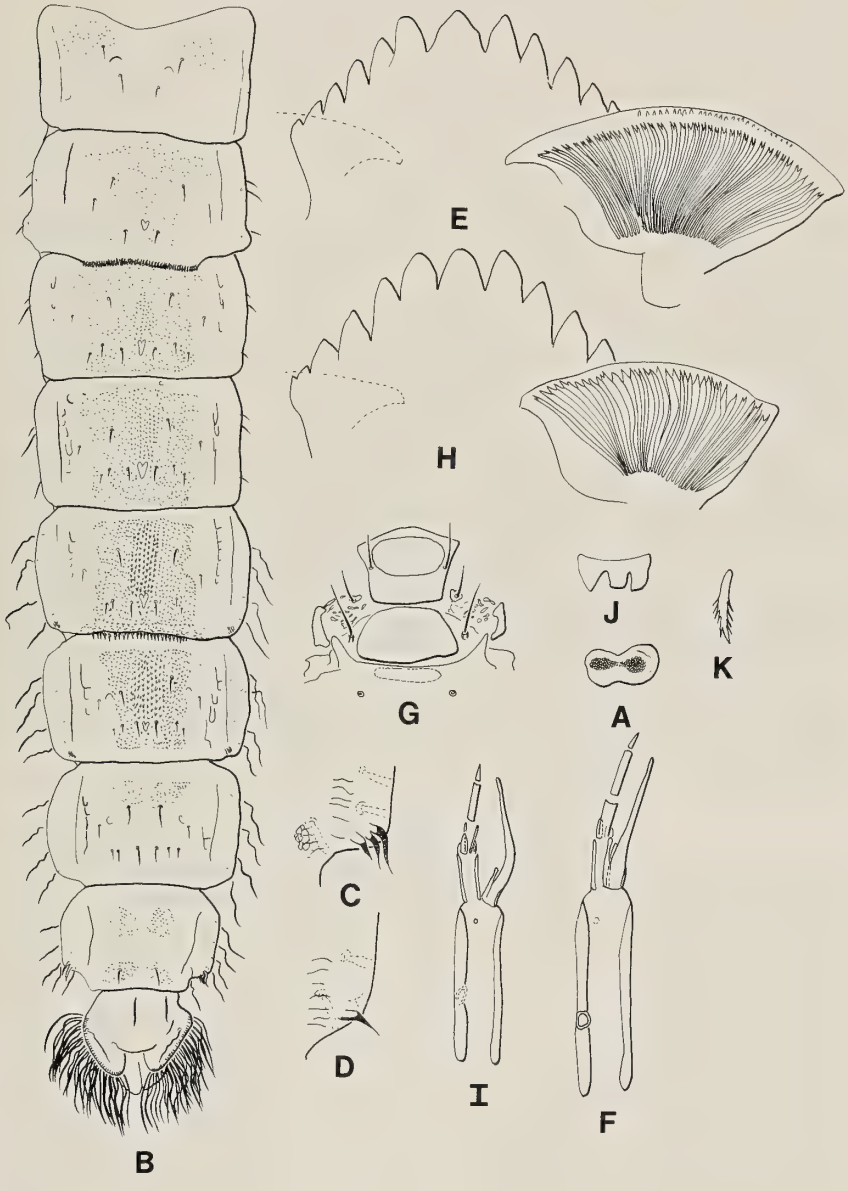
FIG. 42. *D. jonmartini,* pupa (A–D) and larva (E-G). A) Thoracic horn base. B) Abdomen, dorsal. C, D) Caudolateral spurs on T VIII. E) Mentum and ventromental plate. F) Antenna. G) Anterior margin of frontal apotome and labral sclerites. *D. sarinae,* larva (H-K). H) Mentum and ventromental plate. I) Antenna. J) Pecten epipharyngis. K) SI.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Chapter V. Zoogeography

Chironomidae are well known for their usefulness in biogeographic studies. Brundin's (1966) classic work demonstrated the hypothesized break up of Gondwanaland with the present day distribution of podonomine chironomids. However, many other groups of chironomids, including *Dicrotendipes,* apparently do not lend themselves well to historical biogeographic work (see Ashe et al. 1987). Brundin (1966) worked mainly with chironomids in the plesiomorphic subfamily Podonominae (the bulk of his 1966 monograph is a taxonomic study on the subfamily); most of the species studied are essentially cold stenotherms restricted to swiftly flowing mountain streams. In contrast, *Dicrotendipes* is cosmopolitan, vagile and inhabits many types of aquatic environments including swiftly flowing streams, ponds, and lakes, and at least 3 species inhabit brackish water salt marshes (Epler 1987a, Hashimoto 1984, Prat 1981). The present day distribution of *Dicrotendipes* shows no correlation with any tectonic movements.

Fossils may sometimes provide clues to a taxon's biogeographic history (Brown & Gibson 1983:249). Although the fossil history of the Chironomidae extends at least to the middle Jurassic to late Cretaceous (summarized by Oliver 1981; see also Ashe et al. 1987), the earliest records of *Dicrotendipes* date only from the late Pleistocene (approximately 10–12,000 years b.p.) (Hofmann 1971a, 1971b, 1978), long after any hypothesized major plate movements. A larval mentum with ventromental plates illustrated by Hofmann (1971b:fig. 19) appears to be a *D. modestus* or *D. tritomus.* Thus the fossil record to date provides no indication of the historical biogeography of the genus.

Distribution Patterns

There are some interesting distribution patterns in the genus, which are summarized and illustrated in the remainder of this chapter. Several papers have been published which deal with distribution patterns in the Chironomidae (Ashe et al. 1987; Fittkau 1980; Fittkau & Reiss 1978, 1979; Reiss 1977b, 1978; Reiss and Sublette 1985). Distribution records recorded in this chapter are taken from these papers, specimens examined for this study, papers with new distribution records (Hashimoto et al. 1981; Reiss 1986; Sasa & Hasegawa 1983) and previous revisions/descriptions (Contreras-Lichtenberg 1986; Epler 1987a, 1987b; Freeman 1957, 1961a).

I am utilizing the faunal regions as delimited in Pielou (1979:8), except that I use Afrotropical instead of Ethiopian (following Freeman & Cranston 1980 and Ashe et al. 1987).

Holarctic. Four species display a Holarctic distribution: *D. lobiger* (Fig. 43), *D. modestus* (Fig. 44), *D. nervosus* (Fig. 45) and *D. tritomus* (Fig. 46).

Pan-American. The *D. californicus* complex (*D. californicus, D. crypticus, D. embalsensis, D. obrienorum & D. pellegriniensis*) shows a western pan-American distribution pattern (Fig. 47). Some other chironomid species have a distinct pan-American distribution, i.e., *Goeldichironomus holoprasinus* (Goeldi), *G. amazonicus* (Fittkau), *G. carus* (Townes) and *Caladomyia* spp. (Reiss & Sublette 1985). If I am correct in my determination of a solitary larva from Paraguay as *D. crypticus* (see Chapter III, the specimen may be a *D. embalsensis*), this species displays an interesting disjunct distribution (Fig. 47). This distribution, as well as the apparent restriction of *D. californicus* to the west of the Andes (*D. pellegriniensis* may be a form of *D. californicus;* see Chapter III), may merely represent the relatively meager amount of chironomid collecting done in the Neotropics outside of the Amazon region. See also remarks under each species of the *D. californicus* complex in Chapter III.

Dicrotendipes aethiops has a southwestern U.S.-Mexican distribution, but apparently does not occur in the Neotropical region; *D. sinoposus* occurs in Mexico, northern South America and the Caribbean (Dominica), but does not occur in the Nearctic region (Fig. 48).

Palaearctic-Afrotropical. Several species are found in both of these biogeographic regions: *D. septemmaculatus* (Fig. 49), *D. fusconotatus* (Reiss 1977b; Contreras-Lichtenberg 1986) and *D. peringueyanus* (Prat 1981; Contreras-Lichtenberg 1986).

Pan-Palaeotropical. *Dicrotendipes septemmaculatus* (Fig. 49) is found throughout the tropics of the Old World, extends to southern Europe and Japan to the north, and is also found in north and south Australia. Along with *D. modestus* and *D. nervosus,* it is among the most widely distributed species of the genus in the world.

Species with deeply bifid inferior volsellae are distributed pantropically. However, I believe the Neotropical species with bifid inferior volsellae represent a different lineage, probably apomorphic, from the Afrotropical species with similar inferior volsellae. Until associated larvae of the Neotropical species are examined, such a hypothesis must remain a conjecture. Neotropical adults (with bifid inferior volsellae) all possess palmate sensilla chaetica on the hind metatarsus (absent on Afrotropical species). The pupae of the only 2 Neotropical species possessing bifid inferior volsellae with known pupae have 4 lateral lamellar setae on T VIII (5 in Afrotropical species) and lack anal lobe shagreen (present on Afrotropical forms). At least 2 hypotheses may explain the occurrence in the Neotropics of *Dicrotendipes* with deeply bifid inferior volsellae: 1) a vicariance hypothesis in

which the Neotropical lineage is directly descended from the Afrotropical linege; after the separation of South America and Africa (there are no data which would indicate that the genus *Dicrotendipes* had yet evolved at this period of time) the lineage evolved to the apparent apomorphic state of 4 lateral setae on pupal T VIII and a reversal occurred with the palmate sensilla chaetica on the hind metatarsus; 2) a dispersal hypothesis in which the Neotropical lineage is descended from a more apomorphic Nearctic lineage which dispersed south and then developed the palmate sensilla chaetica on the hind metatarsus. Perhaps some environmental factor in the tropics influences the genome to produce a phenotype with deeply bifid inferior volsellae. More larvae and pupae, currently unknown, of other species from the neotropics must be examined to test these hypotheses. The V-shaped median shagreen area on pupal T VI of *D. fittkaui* and *D. soccus* may ally these 2 Neotropical species with deeply bifid inferior volsellae with the Holarctic *D. nervosus* group. Such an alliance would provide support for the dispersal hypothesis concerning the distribution of species with deeply bifid inferior volsellae.

Oriental-Australasian. In addition to the afore-mentioned *D. septemmaculatus,* 3 other species range across these 2 faunal regions: *D. pelochloris* (Fig. 50), *D. flexus* (Fig. 51) and *D. tenuiforceps* (Fig. 51).

Endemics

Many species are apparently endemic to their regions. These are [(?) indicates a questionable species name]:

Nearctic: *D. adnilus, D. aethiops, D. botaurus, D. fumidus, D. leucoscelis, D. lobus, D. lucifer, D. neomodestus, D. simpsoni, D. thanatogratus* (the last species apparently endemic to Florida).

Neotropical: *D. alsinensis, D. amazonicus, D. dasylabidus, D. demissus, D. embalsensis, D. fittkaui, D. nestori, D. palearivillosus, D. paradasylabidus, D. paterjohni, D. pellegriniensis, D. radinovskyi, D. reissi, D. sinoposus, D. soccus.*

Palaearctic: *D. fusciforceps* (?), *D. inouei, D. notatus, D. pallidicornis, D. tamaviridis, D. truncatus* (?), *D. venetus* (?).

Afrotropical: *D. bredoi, D. chambiensis, D. collarti, D. cordatus, D. ealae, D. freemani, D. kribiicola, D. leucolabis, D. schoutedeni, D. sudanicus.*

Oriental: *D. arcistylus, D. canitibialis, D. semiviridis* (?).

Oceanian: *D. candidibasis.*

Australasian: *D. balciunasi, D. bilobatus, D. conjunctus, D. cumberlandensis, D. jobetus, D. jonmartini, D. leei, D. lindae, D. pseudoconjunctus, D. sarinae, D. taylori.*

Fig. 43: Distribution map for *D. lobiger.*
Fig. 44: Distribution map for *D. modestus.*

43

44

Fig. 45: Distribution map for *D. nervosus.*
Fig. 46: Distribution map for *D. tritomus.*

45

46

Fig. 47: Distribution map for *D. californicus* (●), *D. crypticus* (▲), *D. embalsensis* (*), *D. obrienorum* (■) and *D. pellegriniensis.* (○).

47

Fig. 48: Distribution map for *D. aethiops* (■) and *D. sinoposus* (●).

48

Fig. 49: Distribution map for *D. septemmaculatus.*

49

Fig. 50: Distribution map for *D. pelochloris.*
Fig. 51: Distribution map for *D. flexus* (●) and *D. tenuiforceps* (▲).

50

51

Chapter VI. Phylogeny

A phylogenetic analysis of the species in the genus *Dicrotendipes* was performed utilizing a standard Hennigian cladistic analysis as described by Hennig (1966), Ross (1974) and Wiley (1981).

Saether (1977) provided a cladistic analysis of the genera of the tribe Chironomini, which includes *Dicrotendipes*. He proposed that one synapomorphy, the presence of microtrichia on the well-developed female genitalic apodeme lobe, delimited a group of genera (*Dicrotendipes, Chironomus, Glyptotendipes, Kiefferulus* and *Einfeldia*), with the genera *Nilodorum* and *Goeldichironomus* as their sister group. However, Saether used the species *Nilodorum devineyae* Beck as the representative of *Nilodorum* in his analysis; this species is actually a *Goeldichironomus* (Pinder & Reiss 1983). Saether's "*Goeldichironomus-Nilodorum*" sister-group is actually only *Goeldichironomus*. Similarities in the larvae of *Kiefferulus* and *Nilodorum* led me to believe that *Nilodorum* should actually be included with the same group as *Dicrotendipes, Chironomus, Einfeldia, Kiefferulus,* and *Glyptotendipes*. Through the kindness of Dr. L. Hare, females of "true" *Nilodorum* sensu Pinder & Reiss (1983) (see Ashe et al. 1987:54 for a discussion on the taxonomic status of *Nilodorum*) were made available. *Nilodorum* does possess a well-developed apodeme lobe with numerous well-developed microtrichia, and thus joins the group of genera including *Dicrotendipes, Chironomus, Einfeldia, Glyptotendipes* and *Kiefferulus* (hereafter called the "*Chironomus* group").

Methods

Only 27 species known in all 3 life stages were included in the analysis. This was necessary because in many cases the apomorphy or apomorphies used to delimit lineages was/were present only in one life stage. It is often impossible to identify *Dicrotendipes* to species using only one life stage. This often necessitates rearing larvae through the pupal stage to the adult stage to correctly identify some species. Species descriptions from the literature were not used, because descriptions were incomplete. Many species are not known in all 3 life stages. The *D. californicus* species complex and the *D. lucifer* complex were treated as single taxa, leaving a total of 25 taxa to be analyzed. The 25 species used in the cladistic analysis were (abbreviations used for the species in Fig. 52 are given in brackets): *D. californicus* [CALF], *D. candidibasis* [CAND], *D. conjunctus* [CONJ], *D. cumberlandensis* [CUMB], *D. flexus* [FLEX], *D. fumidus* [FUMI], *D. fusconotatus* [FUSC], *D. jonmartini* [JONM], *D. kribiicola* [KRIB], *D. leucoscelis*

[LEUC], *D. lobiger* [LOBR], *D. lobus* [LOBS], *D. lucifer* [LUCI], *D. modestus* [MODS], *D. neomodestus* [NEOM], *D. nervosus* [NERV], *D. notatus* [NOTA], *D. pallidicornis* [PALL], *D. pelochloris* [PELO], *D. pseudoconjunctus* [PSEU], *D. sarinae* [SARI], *D. septemmaculatus* [SEPT], *D. sudanicus* [SUDA], *D. thanatogratus* [THAN] and *D. tritomus* [TRIT].

Taxa were grouped together on the basis of shared derived characters, termed synapomorphies. The polarity of character states (derived or apomorphic and ancestral or plesiomorphic) was determined by outgroup analysis. If a character existed in a similar state in both the ingroup (the group being analyzed, in this case *Dicrotendipes*) and the outgroup (the *Chironomus* group), that character state was termed plesiomorphic and was not used in the analysis. Symplesiomorphies (shared ancestral character states) are not used because they do not offer phylogenetic information as it applies to the ingroup. Only synapomorphies indicate that taxa may share a direct common ancestor. Symplesiomorphies can be synapomorphies at a different level of universality (Wiley 1981). The character state "female apodeme lobe well developed with numerous microtrichia" is symplesiomorphic for *Dicrotendipes* in relation to the *Chironomus* group. However, it is a synapomorphy for the *Chironomus* group in relation to the tribe Chironomini.

Saether (1977, 1979, 1983, 1986) has postulated that underlying synapomorphies (homoiologous characters of Hennig (1966:17); "the inherited capacity to develop parallel similarities" (Saether 1986:5)) are useful in cladistic analyses, a viewpoint condemned by Farris (1985). Saether (1986) discusses underlying synapomorphies again. I have not used underlying synapomorphies as characters in my cladistic analysis. A problem inherent in using underlying synapomorphies as characters in a cladistic analysis is that one could justify any grouping one desires by declaring any sporadically occurring character state as an underlying synapomorphy. Underlying synapomorphies may provide additional evidence to support hypotheses based on other synapomorphies, but cannot be used as the sole evidence to support an hypothesis.

The outgroup used in the analysis was the *Chironomus* group. Because of taxonomic uncertainty and probable polyphyletic lineages, it was not possible to select a single genus as an outgroup. All of these genera are in great need of revision.

Results and Discussion

The characters and character states used to construct a hypothetical phylogeny of *Dicrotendipes* species known in the adult, pupal and larval

stages are listed below. Furcations in the cladogram (Fig. 52) are indicated by upper case letters; numbers refer to apomorphies (those marked with an * have apparently arisen more than once in different lineages); lower case letters on the tree refer to losses, reversals, possible underlying synapomorphies, or symplesiomorphies and are placed on the tree only for reference purposes and were not used as characters in the cladistic analysis. In the list, lower case letters in parentheses indicate (a) = apomorphic, derived, and (p) = plesiomorphic, ancestral; upper case letters in brackets: [A] = adult character, [P] = pupal character, [L] = larval character.

The first 4 apomorphies listed are synapomorphous for the genus.

1. Pecten epipharyngis with less than 15 lobes (a); more than 15 lobes (p) [L].
2. Ventromental plate ratio less than 2.5 (a); more than 2.5 (p) [L].
3. Thoracic horn base with 2 tracheal bundles (a); 1 tracheal bundle (p) [P].
4. Sternite VI with ventral accessory setae (a); without ventral accessory setae (p) [A].

Saether (1977: Fig. 62) utilized the short, squat larval ventromental plates as his Trend 26 to separate *Dicrotendipes* from the genera *Chironomus, Kiefferulus, Glyptotendipes* and *Einfeldia*. This trend corresponds to apomorphy 2 in this cladistic analysis. Apomorphies 3 and 4 are apparently secondarily lost (reversals have taken place) in several species. The 2 tracheal bundles of the thoracic horn are partially joined by a narrow "bridge" of tracheoles in several species, and in at least 2 species only 1 tracheal bundle is present. Both of these conditions can vary from one side to the other in the same specimen. The ventral accessory setae on S VI have apparently been lost in the *californicus* complex and the *septemmaculatus* group. This apparent lack of setae may be a result of the small sample examined in the *septemmaculatus* group; it is also possible that some populations of a single species lack these setae. This last situation is apparent in several other species (*D. candidibasis, D. lobiger, D. modestus*). However, I have examined hundreds of specimens of the *californicus* complex and have never observed ventral accessory setae on them.

A 5. Acrostichal setal number reduced (a); normal (p) [A].

6. Frontal apotome with large ventral pit present (a); frontoclypeal apotome with large ventral pit present (p) [L].
7. Superior volsella without heavily sclerotized apical projection (a); with heavily sclerotized apical projection (p) [A].

a. S III with needlelike setae [P].

This furcation separates *D. lobiger* from the remaining species in the genus. The presence of a frontoclypeal apotome is plesiomorphous through-

out the Chironominae and apparently in the sister-group, the Orthocladiinae (Cranston, et al. 1983). The presence of a large ventral pit may indicate that *Einfeldia* species group A of Pinder & Reiss (1983) may be the "closest" sister-group to *Dicrotendipes. Einfeldia* is in drastic need of revision and is probably polyphyletic.

The needlelike setae on pupal S III are also found in the *D. modestus* group (furcation U), and in some species in at least one genus in the outgroup, *Kiefferulus. Kiefferulus* is also in need of revision. This character may be an underlying synapomorphy for the group of genera closely related to *Dicrotendipes.*

B 8. Frontal apotome with frontal process (a); frontal apotome with large ventral pit (p) [L].
9. Posterior margin of T V with 2 groups of hooklets (a); without hooklets (p) [P].
37. Shagreen on T VI broadly V-shaped (a); shagreen quadrilateral (p) [P].

Furcations A and B define the 3 main groups (I, II and III, Fig. 52) of species in the genus based on larval and pupal characters. Although other genera in the outgroup have larvae which also possess frontal or fronto-clypeal apotomes with variously sized ventral pits, those present in *Dicrotendipes* are shaped differently and are often located in slightly different areas. The presence of hooklets at the posterior margin of T V is unique among the group of genera.

C*10. Mentum with 6th tooth fused/appressed to 5th (a); mentum without fused/appressed teeth (p) [L].
11. Superior volsella digitiform with ventrally directed membranous apex (a); digitiform without membranous apex (p) [A].
b. T IX with dorsal ovoid area [A].

Apomorphy 10 defines the *leucoscelis*-group. A somewhat similar mental appression/fusion occurs in 2 Nearctic members of the *nervosus* group.

Apomorphy 11 is distinctive for the *conjunctus*-group.

The dorsal ovoid area on T IX is a symplesiomorphy shared with many species of *Chironomus, Einfeldia* and *Kiefferulus.* Its presence on the cladogram is only for reference purposes. In addition to the 3 species of the *conjunctus* group, this character state is also found in *D. pelochloris* in the *pelochloris* group. It occurs sporadically throughout the *Chironomus* group.

D 12. Acrostichal setae absent (a); present (p) [A].
13. Inferior volsella with extremely wide apex (a); normal apex (p) [A].
c. Loss of hooklets on posterior margin of T V [P].

Apomorphies 12 and 13 are autapomorphies for *D. cumberlandensis,* which has apparently undergone a reversal with respect to the posterior hooklets on T V.

E 14. Less than 30 ventromental striae (a); more than 30 striae (p) [L].
15. Superior volsella strongly arched mediad (a); weakly arched or almost straight (p) [A].
d. Palmate sensilla chaetica present on hind metatarsus [A].

Apomorphies 14 and 15 are autapomorphies for *D. pseudoconjunctus.* This species is one of 2 species known outside of the Neotropical region in which palmate sensilla chaetica are present on the hind metatarsus of the male. These sensilla are also present in males of *Chironomus, Einfeldia, Kiefferulus* and *Nilodorum.* Their presence may be an underlying synapomorphy for the "*Chironomus* group." More data are needed.

F*16. Head capsule with grainy integument (a); without grainy integument (p) [L].
17. Superior volsella stout, with expanded apex (a); superior volsella digitiform (p) [A].
18. Anal point wide and strongly deflexed (a); anal point normal (p) [A].

Furcation F splits the *leucoscelis* and *jonmartini* groups from the *pelochloris* group.

G 19. Mentum with 6th, 5th and 4th lateral teeth fused/appressed (a); with only 6th and 5th lateral teeth fused/appressed (p) [L].
e. Palmate sensilla chaetica present on hind metatarsus [A].
f. T IX with dorsal ovoid area [A].
g. Loss of spines on posterior margin of T V [P].

Apomorphy 19 is an autapomorphy for *D. kribiicola.* Apparently 3 reversals have taken place with *D. pelochloris.* It and *D. pseudoconjunctus* possess palmate sensilla chaetica on the male hind metatarsus (see above). The dorsal ovoid area on T IX is also found on the *conjunctus* group and in the outgroup, where it occurs sporadically. *D. pelochloris* has apparently lost the posterior hooklets on T V.

H 20. Inferior volsella with membranous dorsal extension (a); without (p) [A].

I*21. Posterior margin of labral sclerite 1 with low tubercles (a); labral sclerite 1 smooth (p) [L].
*22. T VIII with 4 lateral lamellar setae (a); with 5 setae (p) [P].
23. T V hooklets in continuous row (a); in 2 groups (p) [P].
24. Frontal apotome with reduced ventral pit (a); with large ventral pit (p) [L].
h. Mentum normal.

Apomorphy 21 is autapomorphic (within the *leucoscelis* group) for *D. notatus.* This character state is also found in the *modestus-fumidus* groups.

Apomorphies 22–24 define the *jonmartini* group. Placement of this group is somewhat arbitrary, and is based mainly on the assumption that the 2 posterior groups of hooklets on T V transformed to the single band found in this group, and that the large frontal pit has been reduced to the faint, wide frontal pit found in *jonmartini* and *sarinae*. Based on superior volsella morphology, the 2 unusual species with median volsellae (*D. balciunasi* and *D. lindae*) may belong here, but without the immature stages it is not possible to accurately place them.

I must also assume here that the apomorphic state of 4 lateral lamellar setae on T VIII has evolved twice in the genus, because the character state occurs in 2 different lineages. All other species with 4 setae also possess a frontal projection, sometimes surrounded by a pit. This pit is not similar to, and probably not homologous to, the weak pit found in the *jonmartini* group. I believe it is more likely that the pupa would lose a seta and add a few posterior hooklets on T V (as in the *jonmartini* group), than for the posterior band of hooklets to have arisen twice within the genus.

The presence of a membranous dorsal extension (apomorphy 20), similar to that found on the Palaearctic *D. notatus,* may ally the *jonmartini* group with the *leucoscelis* group. Both groups also share the larval head capsule with a grainy integument, a character which has arisen at least 2 other times in the genus (*fumidus* and the *californicus* complex). Placement of the *jonmartini* group is to be considered tentative. It is also possible that the *jonmartini* group may be more closely allied with the *conjunctus* group, for both groups are exclusively Australian. More data are needed, as the *jonmartini-sarinae* sample size was small (n = 6 larvae and 3 pupae).

J 25. Superior volsella pediform, apex directed mediad (a); superior volsella digitiform (p) [A].

26. Less than 30 ventromental striae (a); more than 30 striae (p) [L].

Apomorphies 25 and 26 are autapomorphies for *D. jonmartini* and *D. sarinae,* respectively.

K*27. T VIII with 4 lateral lamellar setae (a); with 5 setae (p) [P].

28. Anal lobe with shagreen (a); without shagreen (p) [P].

29. Wings with spots (a); wings immaculate (p) [A].

30. Apex of inferior volsella deeply bifid (a); apex clubbed,emarginate-cordiform (p) [A].

31. Superior volsella mostly bare, long cylindrical, curved mediad, with moderately sclerotized apex (a); superior volsella digitiform (p) [A].

i. Loss of S VI ventral accessory setae [A].

Apomorphies 28–31 define the *septemmaculatus* group. I have not observed S VI ventral accessory setae on any members of this group. The

superior volsellar type is unique to this group. Furcations L, M and N split the group into the 4 species whose immature stages are known.

L*32. Mentum with some lateral teeth fused (a); mentum without fusions (p) [L].

j. More than 50 ventromental striae [L].

M 33. Hypopygium with accessory lobes (a); without lobes (p) [A].

N*34. Mandible with lateral teeth modifications (a); without modifications (p) [L].

35. Wing with clouds along veins (a); wing with spots (p) [A].

Apomorphies 32–35 are autapomorphies for species within the *septemmaculatus* group.

O*36. Posterior margin of labral sclerite 1 with low tubercles (a); labral sclerite 1 smooth (p) [L].

38. Superior volsella cylindrical, with membranous apex (a); superior volsella cylindrical, without membranous apex (p) [A].

39. T V with separate anterolateral shagreen areas (a); without separate areas (p) [P].

Furcation 0 is the splitting point for the 2 main lineages with 4 lateral setae on pupal T VIII (with the exception of the *jonmartini* group, which is apparently more closely related to the *conjunctus-leucoscelis* groups). This refers only to those species whose larvae are known. The Neotropical forms with bifid inferior volsellae may also belong here, for the pupae of the two known species have 4 lateral setae on T VIII and the shagreen on T VI is broadly V-shaped. These Neotropical species probably are a sister group to the *nervosus* group.

P*40. 1st and 2nd lateral teeth of mentum fused (a); not fused (p) [L].

41. Proximal inner tooth of mandible modified (a); unmodified (p) [L].

Q 42. Superior volsella deltoid (a); superior volsella cylindrical with membranous apex (p) [A].

Furcations P and Q are to be considered arbitrary, due to the presence of *D. lobus*. This species is difficult to place due to its unusual superior volsella. The V-shaped shagreen on T VI indicates that this species belongs with the *nervosus* group. I have placed *D. lobus* closer to *D. candidibasis* and *D. flexus* (furcation Q) because these 3 species share an apomorphy, the fusion of the 1st and 2nd lateral teeth of the mentum. However, this character is apparently homoplasious, for it appears again in the *modestus* group (*D. neomodestus*) and in the *septemmaculatus* group. It does appear that the fusion in *lobus, candidibasis* and *flexus* is not similar or homologous to the fusion found in the other groups; the fusion of the teeth is more complete in *lobus,* etc. Obviously, more data are needed here.

R 43. Mentum with median tooth sunken well beneath level of 1st lateral teeth (a); median tooth subequal to 1st lateral teeth (p) [L].

44. Wing with bands/spots (a); wing immaculate (p) [A].
*45. Apodeme lobe with few, weak microtrichia (a); with numerous, well developed microtrichia (p) [A].
46. Cephalic tubercles minute (a); well developed (p) [P].
S 47. Superior volsella rotated 90° around longitudinal axis (a); not rotated (p) [A].

Apomorphies 43–47 are autapomorphies for species within the *nervosus* group; 43–45 define *candidibasis,* 46 *flexus,* 47 the *lucifer* complex.

T 48. Superior volsella cylindrical with lightly sclerotized apex (a); with membranous apex (p) [A].
*49. Head capsule with grainy integument (a); without grainy integument (p) [L].
*k. S III with needlelike setae [P].
50. Apotome with small frontal pit surrounding frontal projection (a); with frontal projection only (p) [L].

Apomorphies 48 and 49 are apomorphic for *D. fumidus,* a species intermediate in characters between the *modestus* and *nervosus* groups. Apomorphy 50 is a synapomorphy for the *modestus* group. All species in the *modestus* group also have needlelike spines on pupal S III, a character also found in *D. lobiger* and in the genus *Kiefferulus.* Similar groups of spines are also found on at least one genus outside of the outgroup, *Cladopelma.* This character is not used in this analysis, and is placed on the cladogram for informational purposes only.

U*51. Apodeme lobe with few, weak microtrichia (a); with many, well developed microtrichia (p) [A].
52. Superior volsella pediform (a); cylindrical (p) [A].

Apomorphy 51 delimits the species *D. tritomus* in the *modestus* group. This species does not have a pediform superior volsella (apomorphy 52), but possesses a superior volsella somewhat similar to that of *D. nervosus.* However, closer inspection reveals that the volsellae of the 2 species are not similar (Epler 1987a). Larvae and pupae of *D. tritomus* are almost identical to *D. modestus,* and often are inseparable without associated adults.

V 53. Caudolateral spurs on T VIII located anterior to posterior corner (a); spurs located on posterior corner (p) [P].
*54. Head capsule with grainy integument (a); without grainy integument (p) [L].
*55. Anal lobe with shagreen (a); without shagreen (p) [P].
56. Fewer than 20 ventromental striae (a); more than 20 ventromental striae (p) [L].
*57. 1st and 2nd lateral teeth of mentum fused (a); normal (p) [L].

Apomorphies 53 and 54 are apomorphies for the *D. californicus* complex.

Apomorphies 55 and 56 are autapomorphic for *D. thanatogratus*. Apomorphy 57, a homoplasy, is autapomorphic within the *modestus* group for *D. neomodestus*. There is no unambiguous way to delineate the cladogenesis of these species with current data.

The cladistic analysis indicates that the species fall into the following 9 groups (denoted by numbers above the species names in the cladogram, Fig. 52): 1) *lobiger* group: *lobiger;* 2) *conjunctus* group: *conjunctus, cumberlandensis, pseudoconjunctus;* 3) *pelochloris* group: *kribiicola, pelochloris;* 4) *leucoscelis* group: *leucoscelis, notatus;* 5) *jonmartini* group: *jonmartini, sarinae;* 6) *septemmaculatus* group: *fusconotatus, pallidicornis, septemmaculatus, sudanicus;* 7) *nervosus* group: *candidibasis, flexus, lobus, lucifer, nervosus;* 8) *fumidus* group: *fumidus;* 9) *modestus* group: *californicus, tritomus, modestus, neomodestus, thanatogratus.*

Epler (1987c) used the computer program PAUP (Swofford 1985) as a supplemental tool in phylogenetic analysis. The PAUP analysis basically agreed with the Hennigian cladistic analysis. PAUP constructs trees utilizing the Wagner method and a maximum parsimony algorithm, i.e., the tree with the fewest steps (character state transformations) is the most parsimonious. If one assumes that the Hennigian cladogram that invokes the smallest number of hypotheses to deal with homoplasy (convergence/parallelism: the occurrence of similar character states in species which do not share an immediate common ancestor possessing that character state) is the most parsimonious, trees constructed from the same data should yield similar results (Swofford 1985). Some workers contend that the use of Wagner trees and computer programs reduces bias and promotes objectivity (Farris 1985; see also Saether 1986). However, one begins to introduce bias when the characters for the analysis are chosen (all the potential characters of an organism are not used), and, as Saether (1986:3) stated: "there is no biological evidence that minimum length trees or equally parsimonious trees are most in accordance with the "true" tree." To invoke strict parsimony to explain evolutionary relationships could mean that evolution as a process "knows" the shortest path to take to reach a given goal. Hennig (1966) did not advocate the use of parsimony to resolve conflicts in a cladogram, but instead recommended that the full set of characters be reexamined to determine if characters had been misinterpreted. I believe that it is the taxonomic precision of the worker and his/her knowledge of the group(s) in question that can decide the usefulness and "correctness" of the hypothesized cladogram(s).

The 3 major lineages (I, II and III in Fig. 52) could be considered subgenera. However, these are based chiefly on characters of the immature stages (mainly the larval frontal/frontoclypeal apotome). It is impossible in many

cases to place adults in subgenera, and the majority of *Dicrotendipes* species are known only as adults. For this reason I am not establishing subgenera at this time.

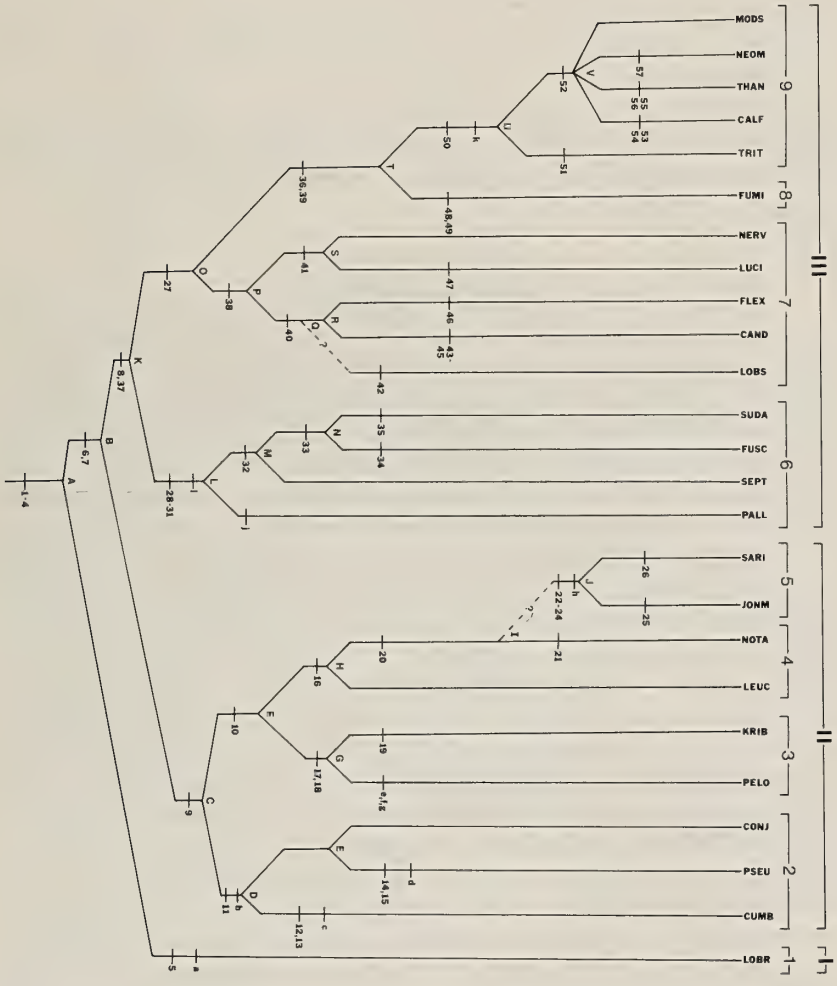

Fig. 52: Cladogram depicting the hypothesized relationships within *Dicrotendipes*.

It is possible to subjectively place some species in some species groups. *Dicrotendipes adnilus, D. sinoposus* and the other 3 members of the *californicus* group (*D. embalsensis, D. obrienorum, D. pellegriniensis*) belong in the *modestus* group; *D. peringueyanus* to the *septemmaculatus* group; *D. balciunasi* and D. *lindae* to the *jonmartini* group; *D. aethiops, D. freemani, D. chambiensis, D. inouei* and *D. tamaviridis* in the *nervosus* group. The majority of the Amazonian species described in Chapter III probably represent another lineage near or derived from the *nervosus* group, based on the pupal characters of *D. fittkaui* and *D. soccus.*

The discovery of the presently unknown immature stages of most *Dicrotendipes* species, especially the Afrotropical and Neotropical species, and revisions of the genera in the *Chironomus* group will greatly improve the taxonomy of the genus.

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Appendix 1

List of recognized species' names in the genus *Dicrotendipes,* and their distribution. (?) indicates a questionable species name. Abbreviations for zoogeographical regions are as follows: NE = Nearctic, NT = Neotropical, PA = Palaearctic, AF = Afrotropical, OR = Oriental, AU = Australian, OC = Oceanian.

D. adnilus Epler NE
D. aethiops (Townes) NE
D. amazonicus Epler NT
D. alsinensis (Paggi) NT
D. arcistylus Guha, Das, Chaudhuri & Choudhuri OR
D. balciunasi Epler AU
D. bilobatus Kieffer AU
D. botaurus (Townes) NE
D. bredoi (Goetghebuer) AF
D. californicus (Johannsen) NE, NT
D. candidibasis (Edwards) OC
D. canitibialis Guha, Das, Chaudhuri & Choudhuri OR
D. chambiensis (Goetghebuer) AF
D. collarti (Goetghebuer) AF
D. conjunctus (Walker) AU
D. cordatus Kieffer AF
D. crypticus Epler NE, NT?
D. cumberlandensis Epler AU
D. dasylabidus Epler NT
D. demissus Epler NT
D. ealae (Freeman) AF
D. embalsensis Paggi NT
D. fittkaui Epler NT
D. flexus (Johannsen) OR, AU
D. freemani Epler AF
D. fumidus (Johannsen) NE
D. fusciforceps (Kieffer) (?) PA
D. fusconotatus (Kieffer) AF, PA
D. inouei Hashimoto PA
D. jobetus Epler AU
D. jonmartini Epler AU
D. kribiicola (Kieffer) AF
D. leei (Freeman) AU
D. leucolabis Kieffer AF
D. leucoscelis (Townes) NE
D. lindae Epler AU
D. lobiger (Kieffer) NE, PA
D. lobus (Beck) NE
D. lucifer (Johannsen) NE
D. milleri (Townes) NE
D. modestus (Say) NE, PA
D. neomodestus (Malloch) NE
D. nervosus (Staeger) NE, PA
D. nestori Paggi NT
D. nigrolineatus (Freeman) AF
D. notatus (Meigen) PA
D. obrienorum Epler NT
D. palearivillosus Epler NT
D. pallidicornis Goetghebuer PA
D. paradasylabidus Epler NT
D. paterjohni Epler NT
D. pellegriniensis Paggi NT
D. pelochloris (Kieffer) OR, PA, AU
D. peringueyanus Kieffer AF, PA
D. pseudoconjunctus Epler AU
D. radinovskyi Epler NT
D. reissi Epler NT
D. sarinae Epler AU
D. schoutedeni (Goetghebuer) AF
D. semiviridis (Kieffer) (?) OR
D. septemmaculatus (Becker) PA, AF, OR, AU
D. simpsoni Epler NE
D. sinoposus Epler NT
D. soccus Epler NT
D. sudanicus (Freeman) AF
D. tamaviridis Sasa PA
D. taylori (Freeman) AU
D. tenuiforceps (Kieffer) OR, AU
D. thanatogratus Epler NE
D. tritomus (Kieffer) PA, NE
D. truncatus (Kieffer) (?) PA
D. venetus (Marcuzzi) (?) PA

Appendix 2

List of recent name changes and current name as recognized in this paper

Previous Name	Current Name
binotatus Kieffer, 1911 (*Chironomus*)	*D. freemani,* nom. nov.
figueroai Vargas, 1952 (*Tendipes* (*Limnochironomus*))	*D. aethiops* (Townes, 1945)
formosanus Kieffer, 1916 (*Dicrotendipes*)	*D. septemmaculatus* (Becker, 1908)
frontalis Kieffer, 1916 (*Dicrotendipes*)	*D. septemmaculatus* (Becker, 1908)
hirtitarsis Johannsen, 1932 (*Chironomus*)	*D. septemmaculatus* (Becker, 1908)
hoonsooi Ree, 1981 (*Kimius*)	*D. pelochloris* (Kieffer, 1912)
incurvus Sublette, 1964 (*Chironomus* (*Dicrotendipes*))	*D. tritomus* Kieffer, 1916
inferior Johannsen, 1932 (*Chironomus*)	*D. pelochloris* (Kieffer, 1912)
innisfailensis Freeman, 1961 (*Chironomus* (*Dicrotendipes*))	*D. tenuiforceps* (Kieffer, 1913)
loripes Guha & Chaudhuri, 1981 (*Xenochironomus*)	*D. pelochloris* (Kieffer, 1912)
melanocnemis Edwards, 1928 *(Chironomus)*	*D. candidibasis* (Edwards, 1924)
niveicauda Kieffer, 1921 (*Limnochironomus*)	*D. pelochloris* (Kieffer, 1912)
paxillus Guha, Chaud, & Nandi, 1982 (*Dicrotendipes*)	*Chironomus glauciventris* (Kieffer, 1912)
pulsus Walker, 1856 (*Chironomus*)	*D. modestus* (Say, 1823)
? *punctatipennis* Kieffer, 1910 *[Chironomus* (*Prochironomus*)]	*D. septemmaculatus* (Becker, 1908)
rajasthani Singh & Kulshrestha, 1977 (*Dicrotendipes*)	*D. septemmaculatus* (Becker, 1908)
socionotus Guha, Chaud. & Nandi, 1982 (*Dicrotendipes*)	*Chironomus* tainanus (Kieffer, 1912)
wirthi Freeman, 1961 (*Chironomus* (*Dicrotendipes*))	*D. pelochloris* (Kieffer, 1912)

The species *Dicrotendipes crispi* (Freeman, 1957), *D. multispinosus* (Freeman, 1957), *D. penicillatus* (Freeman, 1957) *D. regalis* (Goetghebuer, 1936) are no longer considered members of *Dicrotendipes,* and must be assigned to a new, as yet undescribed, genus.

INDEX

Synonyms in *italics,* new species in **boldface**

? *aequatoris, Poly.* — 40
aethiops, Di. — 60
alsinensis, Di. — 60
amazonicus, Di. — 65

balciunasi, Di. — 113
bilobatus, Di. — 115
binotatus, Ch. — 36
bredoi, Di. — 33

californicus, Di. — 61
Calochironomus — 9
candididbasis, Di. — 117
chambiensis, Di. — 34
Cladotendipes — 9
collarti, Di. — 35
conjunctus, Di. — 121
cordatus, Di. — 35
crypticus, Di. — 61
cumberlandensis, Di. — 125

dasylabidus, Di. — 67
demissus, Di. — 68
Dicranotendipes — 9
Dicrotendipes — 9

ealae, Di. — 36
embalsensis, Di. — 62

figueroai, Tend. (Limn.) — 60
fittkaui, Di. — 70
flexus, Di. — 128
forficula, Di. — 37
formosanus, Di. — 42
freemani, Di. — 36
frontalis, Di. — 42
fusconotatum, Calo. — 37
fuscanotatus, Di. — 37

griseonotatus, Calo. — 37
griseoparsus, Calo. — 37
griseovittatum, Poly. — 41

hirtitarsis, Ch. — 42
hoonsooi, Kim. — 134

inferior, Ch. — 134
innisfailensis, Ch. (Di.) — 145

jobetus, Di. — 130
johnmartini, Di. — 131

Kimius — 9
kribiicola, Di. — 39

leei, Di. — 133
leucolabis, Di. — 40
Limnochironomus — 9
Limnotendipes — 9
lindae, Di. — 133
loripes, Einf. — 134
loripes, Xen. — 134

melanochnemis, Ch. — 117

nervosus, Di. — 63
nestori, Di. — 63
nigrolineatus, Di. — 40
nilicola, Di. — 37
niveicauda, Limn. — 134

obrienorum, Di. — 63

palearivillosus, Di. — 72
paradasylabidus, Di. — 73
paterjohni, Di. — 74
pellegriniensis, Di. — 64
pelochloxis, Di. — 134
peringueyanus, Di. — 41
pictipennis, Di. — 42
pictus, Parat. — 35
pilosimanus, Di. — 42
pseudoconjunctus, Di. — 139
punctatipennis, Ch. (Pro.) — 42

quatuordecimpunctatum, Poly. — 42
quatuordecimpunctatus, Di. — 42
quatuorpunctatum, Poly. — 37

radinovskyi, Di. — 76
rajasthani, Di. — 42
reissi, Di. — 76

sarinae, Di. — 142
schoutedeni, Di. — 41
semiviridis, Di. — 145
septmmaculatus, Di. — 42, 145

Sernowia — 9
sexnotatus, Stict. — 42
seychelleanus, Ch. — 36
sinoposus, Di. — 64
soccus, Di. — 78
speciosus, Di. — 42
sudanicus, Di. — 46
tenuiforceps, Di. — 145
?*trilabis, Di.* — 37

wirthi, Ch. (Di.) — 134

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REVISION OF THE MILLIPED FAMILY EURYMERODESMIDAE (POLYDESMIDA: CHELODESMIDEA)

By
Rowland M. Shelley

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BY

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ABSTRACT — *Eurymerodesmus* Brolemann, the sole genus in the chelodesmoid milliped family Eurymerodesmidae, is a speciose mosaic complex that covers a substantial part of the central, south-central, and southeastern United States. It is the dominant polydesmoid in prairie ecosystems, and forms occur in diverse biotopes in both mesic and arid environments. Autapomorphies include a ventral mandibular ridge and medial projection in both sexes; elaborate, hirsute gonopodal apertures; laterally oriented gonopods; simple, unmodified telopodites; and long, silken prefemoral hairs. *Eurymerodesmus* contains 25 species, five of which, *elevatus, caesariatus, crassatus, dactylocyphus,* and *clavatus,* are newly described. *Kewanius* and *Paresmus,* both authored by Chamberlin, are placed in the generic synonymy, and the following species-group names are assigned to specific synonymies: *Paresmus columbus* Causey; *E. bentonus, plishneri, spectabilis,* and *wellesleybentoni,* all by Causey; *creolus* and *schmidti,* both by Chamberlin; and *hamatilis* and *minimus,* both by Loomis. *Eurymerodesmus booneus* Chamberlin is a synonym of *Auturus evides* (Bollman). *Eurymerodesmus christianus* and *louisianus,* both by Chamberlin, are reduced to subspecies of *E. varius* (McNeill); *E. planus* Causey is a race of *E. birdi* Chamberlin. The genus is divided into four lineages, three of which, the *hispidipes, birdi,* and *melacis* lines, are composed of one species group each; the *Kewanius* lineage is comprised of four species groups. Relationships among the lineages are *melacis* + *(hispidipes* + *(birdi* + *Kewanius))*. Along with *Sigmoria, Eurymerodesmus* directs attention to the evolutionary dynamics of mosaic complexes in the Diplopoda and their potential utility as new investigative subjects that may hold more inherent appeal to other biologists than traditional milliped taxonomy.

INTRODUCTION

The central, south-central, and southeastern United States — from northeastern Nebraska, central Illinois, and southeastern North Carolina to the Rio Grande and north Florida (Fig. 1) — is home to the Eurymerodesmidae (Polydesmida: Chelodesmidea). Sympatric through much of this area with eastern Nearctic components of the chelodesmoid families Xystodesmidae and Platyrhacidae, some of whose species they superficially resemble in external body form, eurymerodesmids inhabit a diversity of biotopes including mesic deciduous forest litter in Illinois, the Ozark Plateau, and the Ouachita Physiographic Province; under logs in xeric, sandy, southeastern environments; and under logs and dung in grasslands of the Central Plains. They are the dominant polydesmoid diplopods in prairie ecosystems, ranging westward onto the Edwards Plateau and across the Pecos River in central and southern Texas.

The Eurymerodesmidae is one of the best defined chelodesmoid families, but its affinities within the suborder are obscure. Autapomorphies include a ventral ridge along the mandibular stipes in both sexes that extends into a medial projection, usually larger in males; laterally oriented gonopods with the cannulas located ventrolaterad on the coxa instead of mediad; simple, unmodified, and caudally, instead of anteriorly, projecting telopodites; highly modified and variable gonopodal apertures with relatively unmodified, simple gonopods, instead of vice versa; a variably hirsute aperture indented anteromediad, instead of glabrous and not indented; and extremely long, silken prefemoral hairs, in some forms nearly half as long as the telopodite, extending in variable numbers and arrangements along the stem of the structure, rather than short hairs chiefly restricted to the basal region. The most striking features of eurymerodesmids are the variable aper-

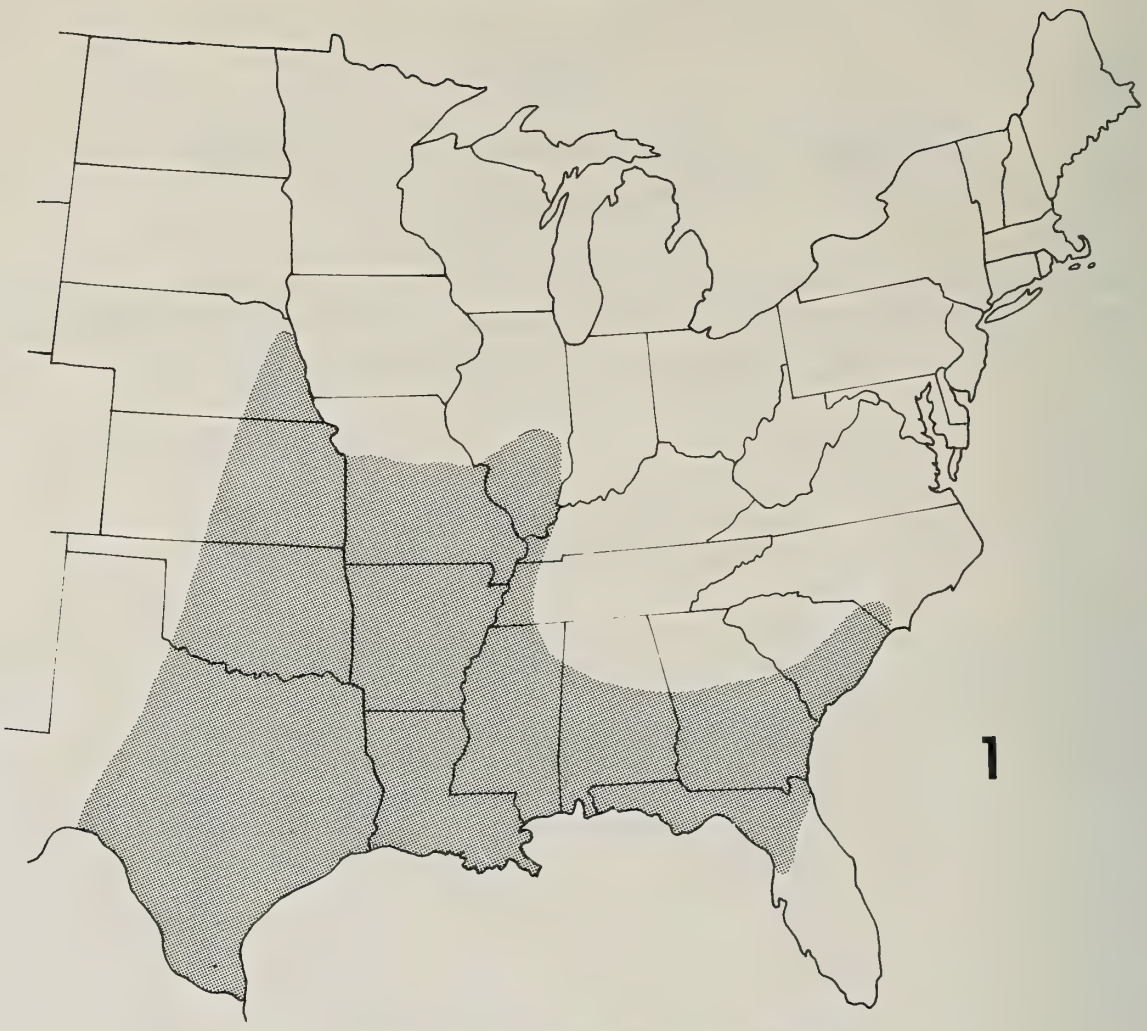


Fig. 1. Distribution of *Eurymerodesmus* and the Eurymerodesmidae.

tures, many of which are elaborately complex. *Eurymerodesmus mundus* and western populations of *E. birdi birdi,* both authored by Chamberlin (1931), exhibit enormous lobes on the caudal aperture margins that extend well below the levels of the ambulatory coxae and must therefore affect either locomotion, posture, or both (Figs. 149-151, 169-171). From spatial considerations, these species must walk "higher" for the lobes to clear the substrate. In some species lacking lobes, for example *E. oliphantus* Chamberlin, *newtonus* Chamberlin, *amplus* Causey, *varius* (McNeill), and *angularis* Causey, the sides of the apertures are divided near midlength thus forming two lateral margins along the caudal halves. The "inner lateral margin" extends variably into the opening and the "outer lateral margin" flares variably laterad thereby enclosing a cavity or "pouch" at the caudolateral corners (Figs. 18, 21, 23, 25, 56, 59, 62, 64, 68, 73, 76-78, 84, 91). The pouches vary from open to closed depending upon the degree that the outer lateral margin leans mediad over them, and they give rise to variable tufts of hairs. Another species, *E. dactylocyphus* n. sp., lacks both of these features but possesses an exceptionally broad aperture with variably elongate flanges at the caudolateral corners; in some individuals the opening covers nearly the entire ventral breadth of the segment (Fig. 184). The anatomical wonders are not limited to males; females of *E. dactylocyphus, angularis, compressus* Causey, *impurus* (Wood), and *crassatus* n. sp. possess dactyliform projections on the cyphopod valves (Figs. 14, 27, 30, 35, 130, 187) that extend caudad in *dactylocyphus* and *compressus* well beyond the aperture margin, overlapping the succeeding two or three segments. They are so long in

some forms of *dactylocyphus* as to resemble supernumerary walking legs. When I first viewed them, I thought the specimen was a mutant. These extreme genitalic modifications in both sexes are so bizarre as to compel speculation on evolution and function, which I think relate to the recent theory of sexual selection by females propounded by Eberhardt (1985) (see sexual selection section, p. 41). Beyond these striking autapomorphies, I am equally impressed with the general hairiness of eurymerodesmids, some forms being extremely setose ventrally. The lobes in *mundus* and *b. birdi* are so densely hirsute as to obliterate the surface, and in some forms of the latter the hairs become progressively longer distad with the apical hairs being fully as long as the lobes themselves, thus effectually doubling the lengths of the structures (Fig. 155). Likewise, the tufts from the caudolateral pouches are extremely dense in some species, and in others the entire aperture margins are variably hirsute, sometimes densely so. Thus in some individuals of *oliphantus,* there are long hairs arising from the anterior and lateral rims, the outer surfaces of the sides extending well onto the metazonum, dense tufts from within the pouches, additional hairs from the inner surfaces of the outer lateral and caudal margins, and still more arising from beneath the division points on the sides (Fig. 91). In addition to these aperture hairs, there are variable and often dense tufts from sternal projections on pregonopodal and postgonopodal segments, even on relatively flat caudal segments and on females. Coupled with those on the gonopods, the overall effect of these hairs and their variations in lengths and densities is so impressive as to be a fitting source for the family-group and type genus names if the millipeds were newly discovered. *Eurymerodesmus* (-idae), literally meaning broad, unit, chain, does not begin to do justice to the anatomical marvels of these arthropods.

In addition to their unique anatomical features, eurymerodesmids are of exceptional ecological interest, because of the aforementioned diversity of their biotopes and their unusual ability to tolerate extremely arid conditions. I encountered a sizeable population of *varius varius* under a sun-baked log on dry sandy soil in Gilchrist County, Florida, and have visited areas in central and southern Texas known to harbor epigean populations of *E. melacis* Chamberlin and Mulaik that can only be described as desert. Had I not known of the presence of *melacis,* I would have sworn that the only possible epigean diplopods in these sandy, sagebrush environments would be desert-adapted spirostreptoids and spiroboloids. At the opposite moisture extreme, I have also collected *v. varius* from wet soil in hardwood hammocks in north Florida and *oliphantus* from a stump in a mesic deciduous woodland in southern Illinois. Likewise, I have visited areas in the Ozark and Ouachita Provinces that would be expected to contain many eurymerodesmids and diverse diplopod faunas because of the moist conditions and abundance of deciduous trees. Suffice it to say that eurymerodesmids have broad ecological tolerances, and of particular interest to North America is their abundance in the Central Plains, where they are the dominant polydesmoids.

Eurymerodesmids are among the earliest described American millipeds. The type species of the type genus, *E. hispidipes* (Wood 1864), proposed for a form from Illinois, was among the first millipeds named by an American author and one of the first species described from the New World. With over 2,000 preserved specimens, eurymerodesmids are abundantly represented in major institutional repositories in the United States, and many colleges and universities within the range have samples in insect and invertebrate collections. Despite this material and the considerable attention it has received in over 40 publications, the Eurymerodesmidae is also one of the most poorly understood of the major Nearctic milliped taxa. Thirty-two species-group names have been proposed, but only two can be confidently identified from published diagnoses. The descriptive accounts are among the worst ever published on the North American fauna, revealing little effort to identify taxonomically important structures or assess their conditions throughout the family. Likewise, the illustrations do not begin to portray diagnostic features, particularly of the apertures. Three species — *E. simplex* Chamberlin, *impurus,* and *melacis* — have not been figured, and most drawings of other species are meaningless sketches. A host of synonyms therefore exists, as few specimens or accounts were consulted before new names were validated. Finally, the general commentary is so riddled with contradictions, conflicting opinions, and outright errors that eurymerodesmid literature is not only useless but actually hinders study. It would be far easier to start with nothing than to have to determine synonymies and untangle such nomenclatorial confusion.

The taxonomic disarray results from two factors. First, like *Abacion* (Shelley 1984a) and several other Nearctic taxa, only one species was assumed to exist for many years, and this name

was routinely applied to forms throughout the generic range. Thus, *hispidipes* has been erroneously assigned to forms from Arkansas, Kansas, Louisiana, Texas, and even Illinois as recently as 1969. Since much of this material is lost, we can only infer which species actually were represented. Secondly as stated earlier, the male gonopods alone are not the principle taxonomic structures at the specific level, unlike most polydesmoid families. Specific details obtain chiefly either in the configuration of the gonopodal aperture, which extends anteriad and compresses the prozonum into a narrow band, or in that plus aspects of the gonopods, which lack a prefemoral process. Somatically, the collum is moderately enlarged; the caudolateral corners of the paranota are broadly rounded; and the epiproct is pointed and subtriangular as in the Xystodesmidae. Eurymerodesmids vary in size from minute specimens of *v. varius* and *melacis* to such large species as *E. goodi* Causey and *dubius* Chamberlin. They tend to be smaller than most sympatric xystodesmids, but the general facies are so similar that mature specimens can easily be mistaken for juveniles of the latter. Juveniles of both families are practically indistinguishable. Despite this resemblance, the families are rarely mixed in the same sample because of their staggered life histories. Eurymerodesmids are decidedly "cold-adapted," most collections occurring between late October and early April (Fig. 210). Conversely, most xystodesmids prefer the warmer weather of late spring, summer, and early autumn. Thus, although sympatric through much of the midwestern and southeastern states, the two families tend to appear at different times of the year.

A curious feature of eurymerodesmids is their stiff, inflexible body; most I have found were tightly coiled in upper humus layers. They die and are preserved in this position, and in contrast to xystodesmids and platyrhacids, are nearly impossible to uncurl without breakage at one or more segmental junctures. Few specimens remain intact after handling or can be unrolled without breakage. Indeed, the exoskeleton will often tear or shatter before adjacent segments can be separated, and length measurements are difficult to obtain. Many workers obviously did not try to uncurl specimens, as evidenced by the unusually high percentage of sexing errors. Segment 7 is overlapped by legs from other segments, and since the gonopodal telopodites are linear and project almost directly caudad, they are inconspicuous laterally in a tightly coiled male. Hence, these specimens are easily mistaken for females, because every segment appears to possess two pairs of legs and there are no obvious gonopods or gaps for the same. Consequently, many "female allotypes" are really male paratypes, and I know of no other helminthomorph milliped group in which so many sex notations are wrong. However, with experience and close observation, one can detect a slight gap between the legs on segment 7 and the raised aperture inside. Males also have a decidedly "flatter" appearance than females, as the paranota are broader and less depressed.

As currently understood (Hoffman 1979), the Eurymerodesmidae consists of two valid genera, *Eurymerodesmus* Brolemann (1900) and *Paresmus* Chamberlin (1942a). A third genus-group name, *Kewanius* Chamberlin (1938), was correctly synonymized with *Eurymerodesmus* by Causey (1963) and accepted by Hoffman (1979). The two valid genera are distinguished solely by the stouter telopodite of *Paresmus,* and *Eurymerodesmus* therefore contains everything that cannot be placed in the former. This distinction is unsatisfactory, since eurymerodesmid telopodites vary considerably in both length and breadth. Thus, major objectives of this revision are detailed analyses of the taxonomically important characters, and decisions on the number of component genera and the status of *Paresmus.* This genus is distinguished more by a subterminal acropodite than by breadth of the telopodite, but this condition blends into the smoothly continuous, broadly terminal acropodite of *Eurymerodesmus* through the intermediate condition represented by the type species of *Kewanius,* a narrowly terminal, discontinuous, and sharply demarcated acropodite. Hence, I regard the family as monotypic and place *Paresmus* and *Kewanius* in synonymy under *Eurymerodesmus,* which I divide into four lineages based on gonopodal features and the configurations of the apertures. These categories correspond to the subgenera or major components of *Sigmoria* (Shelley and Whitehead 1986), but I do not officially designate them as subgenera because genus-group names are only available for two. Since many new forms obviously await detection, it seems best not to validate names that may be overturned by future discoveries. Three of the lineages contain a single species group and are named for the oldest component species, which is anatomically characteristic for the assemblage; *hispidipes* constitutes a separate species group and lineage by itself,

since I cannot relate it to another congener. The fourth lineage, containing 17 species in four species groups, includes those assigned to both *Kewanius* and *Paresmus,* and hence is named the *Kewanius* lineage since there is no characteristic species and this name has priority by four years. Species groups within the *Kewanius* lineage are named for the oldest component species.

I present (Fig. 215) a diagram that I think reflects relationships among the lineages, but none of the sister branches can be unequivocally defined by autapomorphies, demonstrated by all component forms. Unique features can only be suggested for the *melacis* line. Decisions on polarities are hampered by insufficient knowledge of potential out-groups, but I think these traits are plesiomorphies rather than apomorphies. However with the possible exception of the *hispidipes* branch, the lineages are all cohesive geographic entities, partly sympatric with each other. The *birdi* and *Kewanius* lineages are incompletely detached and connect through *polkensis, caesariatus, pulaski,* and *serratus,* all showing acropodal features of the latter and aperture traits of the former. They demonstrate the phenomenon termed "incomplete synapomorphy" in *Sigmoria* (Shelley and Whitehead 1986). The *melacis* branch, however, appears completely segregated, and I consider it sister to the rest of the family.

In conducting this revision, I have attempted to apply the definitions of taxonomic categories employed by Shelley and Whitehead (1986) for *Sigmoria.* However, I have not personally collected many eurymerodesmids, and despite the substantial material, significant collecting gaps occur within the range. Consequently, I cannot determine the nature of the interfaces between many species nor the degree of incipient partitioning. Thus there are problematical areas that cannot be fully resolved in this first revision, for example between *varius* and *amplus* Causey, and among forms of *angularis.* However beyond this purely technical matter, looms the larger question of the actual status of the mostly parapatric forms, both here and within *Sigmoria.* There is no question that *birdi* and *mundus,* broadly sympatric through Kansas, Oklahoma, Texas, and Arkansas, are reproductively isolated and hence full species, but is this true for the parapatric forms in the *Kewanis* and *melacis* lineages, and should they be accorded the same status? Resolution of this question is beyond the scope of this work and requires the attention of someone more versed in theoretical concerns or in reproductive biology of these forms. However, the "species" of the *melacis* and *Kewanius* lineages may actually be only semispecies, with the parent lineage becoming a superspecies. These categories cannot be handled nomenclaturally, so for the present I refer to all parapatric or narrowly sympatric entities that are not interconnected as species. This question bears on the composition of the genus, since I recognize 25 species. If the localized entities are only semispecies, *Eurymerodesmus* may contain as few as five species.

Like *Sigmoria, Eurymerodesmus* is a giant mosaic complex that blankets much of central and southeastern North America. Past workers have extracted pieces of this large puzzle that appear distinct because they possess different combinations of the features of the apertures and gonopods. Consequently, they assigned them different names, thereby adding nomenclatural confusion to an already intricate fauna. I have tried to resolve this difficult problem to the extent possible and leave a stable base for future students. However, the overriding significance of *Eurymerodesmus* and *Sigmoria* is their illumination of mosaics, a widespread phenomenon in the Diplopoda (Shelley 1989). The concluding section therefore attempts to integrate these revisions with recent treatments of other genera and suggest a different emphasis in systematic research that may stimulate interest in diplopodology.

This revision, then, provides complete descriptions or redescriptions of the family Eurymerodesmidae, the genus *Eurymerodesmus,* and all species and subspecies considered valid along with synonymies and pertinent anatomical illustrations. A key has also been formulated to facilitate determinations. A literature review and sections on anatomy and taxonomic characters, and sexual selection precede the systematic accounts, which are followed by sections on ecology, distribution, relationships, and the aforementioned conclusion. All pertinent holotypes or syntypes were examined except those of *compressus* and *Paresmus columbus* and *P. pulaski,* all authored by Causey, which are not at the published repositories and are lost. Also lost is the holotype of *P. paroicus,* whose vial actually contains a male of *Pseudopolydesmus pinetorum* (Bollman). These names were interpreted from near topotypical material, and neotypes are designated for all except *P. columbus,* assigned to synonymy under *dubius.*

In conducting this revision I was fortunate in receiving material from many large and small collections, both institutional and private. Acronyms of sources of preserved study material cited in the text are as follows:

AMNH — American Museum of Natural History, New York, NY.
ANSP — Academy of Natural Sciences, Philadelphia, PA.
CAS — California Academy of Sciences, San Francisco, CA.
EIU — Zoology Department, Eastern Illinois University, Charleston, IL.
FMNH — Field Museum of Natural History, Chicago, IL.
FSCA — Florida State Collection of Arthropods, Gainesville, FL.
ILNHS — Illinois Natural History Survey, Urbana, IL.
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA.
MEM — Mississippi Entomological Museum, Mississippi State University, Starkville, MS.
MNHP — Museum National d'Histoire Naturelle, Paris, France.
MWSU — Zoology Department, Midwestern State University, Wichita Falls, TX.
NCSM — North Carolina State Museum of Natural Science, Raleigh, NC.
NMNH — National Museum of Natural History, Smithsonian Institution, Washington, DC.
OKSU — Biology Department, Oklahoma State University, Stillwater, OK.
RLH — Private collection of Richard L. Hoffman, Martinsville, VA.
SFAU — Biology Department, Stephen F. Austin State University, Nacogdoches, TX.
TAI — Biology Department, Texas A & I University, Kingsville, TX.
TMM — Texas Memorial Museum, University of Texas, Austin, TX.
UGA — University of Georgia Museum of Natural History, Athens, GA.
UMO — Enns Entomological Museum, University of Missouri, Columbia, MO.
UOK — Stovall Museum of Science and History, University of Oklahoma, Norman, OK.
WAS — Private collection of William A. Shear, Hampden-Sydney, VA.
WASU — James Entomological Museum, Washington State University, Pullman, WA.

Literature Review

Although eurymerodesmid millipeds have been known since 1864, when Wood described *Polydesmus hispidipes* from an unspecified site in Illinois, the family Eurymerodesmidae was established only 38 years ago (Causey 1951), nine years after Chamberlin (1942a) proposed the last genus-group name, *Paresmus*. *Eurymerodesmus* Brolemann, 1900, was designated the type-genus. In the original account, *Polydesmus hispidipes* was placed in the nominate subgenus, but the next year Wood (1865) transferred it to the subgenus *Paradesmus* while repeating the verbal description and publishing a gonopod drawing showing the long prefemoral hairs. Wood (1867) described *Polydesmus (Polydesmus) impurus* from material collected at an unspecified locality in Texas by Dr. Gideon Lincecum, a pioneer physician and naturalist. Causey (1952a) reported that Lincecum traveled widely, that his last home was Bonham, Washington County, and that the type locality could not be determined with certainty. However, Bonham is in Fannin County, over 230 miles north of Brenham, the county seat of Washington County, and her error could be in either the town or county. By studying correspondence at the University of Texas library between Dr. Lincecum and Wood, James Reddell (pers. comm.) concluded that the type locality was Long Point, Washington County, near Brenham.

McNeil (1887) described the third eurymerodesmid, *Polydesmus varius,* from a female collected at Pensacola, Escambia County, Florida, and published two cyphopod drawings. Bollman (1888a) transferred *hispidipes* to *Leptodesmus* and noted that it is common throughout Arkansas, but as shown by material at the NMNH, this record refers to *E. pulaski* (Causey), *serratus* n. sp., and perhaps other species. Bollman (1888b) transferred *varius* to *Leptodesmus* and recorded it from Macon, Bibb County, Georgia. In 1893 he included all three previously described species and several xystodesmids as components of *Leptodesmus* and repeated the type localities of each. Two years later, Brolemann (1895) included *hispidipes* in his list of American myriapods and reported it from Louisiana, where it does not occur. As shown by his material at the MNHP, Brolemann's record refers to *E. amplus.*

In 1900, Brolemann proposed *Eurymerodesmus* as a subgenus of *Fontaria.* He illustrated the gonopod of *amplus,* which he misidentified as *hispidipes,* and noted that it did not belong in *Leptodesmus* as previously reported. Since the structure resembled a "secondary branch" of a *Fontaria* gonopod, particularly that of *E. simoni* Brolemann, a synonym of *Harpaphe haydeniana* (Wood), he provisionally included the species in *Fontaria* under the new subgenus. Brolemann listed development of the femur, absence of a "secondary ramus," and the presence of rows of long silken hairs along the "seminal canal" (= prostatic groove) nearly to the tip as diagnostic characters of the new subgenus. Thus, *hispidipes* is the type species of *Eury-*

merodesmus by monotypy, as noted by Jeekel (1971).

In the ensuing decade, Gunthorp (1913) reported *hispidipes* from Cowley, Douglas, and Jefferson counties, Kansas. Since his specimens are lost, I surmise from known records that the Cowley specimen was probably *mundus* and the others were probably *birdi birdi*. Brolemann (1915) elevated *Eurymerodesmus* to generic status and placed it in the tribe Rhysodesmini, subfamily Leptodesminae, family Leptodesmidae. Apparently unaware of Brolemann's work, Chamberlin (1918) recorded *L. hispidipes* from Creston, Natchitoches Parish, Louisiana, a citation based on specimens of *amplus* and *birdi*. Two years later, Chamberlin (1920) acknowledged *Eurymerodesmus* by publishing a brief diagnosis and adding the fourth species, *simplex,* from New Orleans, a locality that is probably wrong.

The period of intensive descriptive work began in 1931, when Chamberlin described *birdi* and *mundus* from Oklahoma, illustrating the gonopods and aperture lobes of each. Chamberlin (1938) established the genus *Kewanius* for *simplex* because of its "glabrous telopodite and larger basal gonopodal division." However, the telopodite, or specifically the prefemur, is really only less densely hirsute than that of *hispidipes,* not glabrous, and the "larger basal gonopodal division" probably refers to the broad clavate condition of the prefemoral stem. Causey (1963) did not think these features warranted generic distinction and placed *Kewanius* in synonymy under *Eurymerodesmus,* an action accepted by Hoffman (1979) and one that I can confirm.

In the decade of the '40's, Chamberlin and Mulaik (1941) described, but did not illustrate, *melacis* from Kerr, Boerne, Hidalgo, Kendall, Bandera, and Concho counties, Texas, without clearly specifying the type locality. Chamberlin (1942a) described and illustrated the gonopods of two new species of *Eurymerodesmus* from both Arkansas and Louisiana — *newtonus* and *oliphantus,* and *creolus* and *louisianae,* respectively — and erected *Paresmus* for a third new species from Louisiana, *paroicus*. Chamberlin (1942b) proposed *E. booneus* for unillustrated specimens from Boone County, Iowa, which are actually juvenile platyrhacids. Thus, *E. booneus* is a junior subjective synonym of *Auturus evides* (Bollman) [syn. nov.!], which is the only platyrhacid in central Iowa and is common in Boone County. Chamberlin (1943) described and illustrated *E. schmidti* and *dubius* from Arkansas, and Loomis (1943) did likewise for *E. minimus,* from Jackson County, Florida. In 1946 Chamberlin proposed and figured *E. christianus,* from Harrison County, Mississippi.

Descriptions of eurymerodesmids increased in the 1950's and were led by six papers by Causey, two the first year. She (1950a) described and illustrated five new Arkansas eurymerodesmids, *E. bentonus, spectabilis,* and *plishneri,* and *Paresmus pulaski* and *columbus,* and reported *E. hispidipes* from Dixon Springs, Pope County, Illinois, a misidentification of *oliphantus*. Later that year Causey (1950b) proposed *E. planus* for a form from Rankin County, Mississippi, and provided a lateral view of segment 7 with the gonopods projecting above the segmental margin. Causey (1951) established the family Eurymerodesmidae, listed several autapomorphies, and described and illustrated *angularis* from Arkansas. The next year Causey (1952a) published diagnoses and drawings of *E. compressus* and *wellesleybentoni,* from Arkansas, and *E. sanbernardiensis,* from Texas, along with a key to the species of *Paresmus* and notes on *P. impurus*. The last species was transferred from *Leptodesmus,* where it had been assigned by Bollman (1893). Causey (1952b) described and illustrated the fifth and final species of *Paresmus, polkensis,* from Polk County, Arkansas, along with *E. goodi* and *amplus* from Arkansas and Louisiana, respectively. This work also included new localities for *birdi, schmidti, mundus, spectabilis,* and *dubius,* a sketch of the aperture of *oliphantus,* mislabeled as *hispidipes,* and the placement of *plishneri* in synonymy under *schmidti*. Chamberlin (1952) reported *melacis* from Uvalde County, Texas, and reiterated the type localities for *dubius* and *schmidti*. Causey (1954) transferred *varius* into *Eurymerodesmus* from *Leptodesmus,* recorded it from Mobile County, Alabama, and placed *minimus* in synonymy, thereby making Loomis' gonopod drawing (1943) the first of a male of *varius*. Chamberlin and Hoffman (1958) listed all eurymerodesmid species to that date with statements of type localities and distributions, and accepted the synonymies of *plishneri* with *schmidti* and *minimus* with *varius*. The last work of the '50's recorded new localities for *melacis* in south Texas (Loomis 1959).

Interest in eurymerodesmids waned after the 1950's. Causey (1963) synonymized *Kewanius* with *Eurymerodesmus* and *spectabilis* with *christianus,* recording new localities for the latter from Louisiana, Alabama, Mississippi, and Arkansas. Next to *hispidipes, spectabilis* was the most widely known species at that time. Loomis (1969) described and illustrated *E. hamatilis* from Angelina County, Texas, and Stewart (1969) recorded *birdi* and

hispidipes from several northeastern Texas counties, the latter being misidentifications of *amplus*. Reddell (1970) reported *Eurymerodesmus* from caves in Bexar, Kerr, and Uvalde counties, Texas, all records of *melacis*. Loomis (1976) proposed the most recent new species, *E. digitatus,* from Burnet County, Texas, and appended a key to species in that state. Hoffman (1978, 1979) considered the Eurymerodesmidae a derivative of the Xystodesmidae and placed both in the superfamily Xystodesmoidea along with the Gomphodesmidae, Campodesmidae, and Oxydesmidae. In the latter work he estimated 22 species for *Eurymerodesmus,* ranging from Georgia to Arkansas and Illinois; *Paresmus* contained five species distributed from Arkansas to Texas.

Thus at this writing, the Eurymerodesmidae consists of two genera, *Eurymerodesmus* and *Paresmus,* with 23 and 5 nominal species, respectively, listed below in chronological order with synonymies, type localities, and other reported counties and states of occurrence. It is noteworthy that 12 species of *Eurymerodesmus* and three of *Paresmus* supposedly occur in Arkansas, while six and one, respectively, have been recorded from Louisiana. Causey (1940) reported *hispidipes* from Duke Forest, Durham County, in central North Carolina, a record deleted by Shelley (1978). *Eurymerodesmus varius* does occur in the southeastern corner of that state but is improbable farther inland as is *hispidipes* anywhere along the Atlantic Coast.

Genus **Eurymerodesmus** Brolemann 1900 (=*Kewanius* Chamberlin 1938)

E. hispidipes (Wood 1864). Illinois without further specification. Erroneously reported from Arkansas and Louisiana in general (Bollman 1888a, Brolemann 1895), and the following states, counties, and parishes: Natchitoches Par., LA (Chamberlin 1918); Cowley, Douglas, and Jefferson cos., KS (Gunthorp 1913); Pope Co., IL (Causey 1950a); and Angelina, Nacogdoches, Rusk, Sabine, Shelby, Smith, and Upshur cos., TX (Stewart 1969).

E. varius (McNeill 1887) (=*E. minimus* Loomis 1943). Pensacola, Escambia Co., FL. Also recorded from Bibb Co., GA (Bollman 1888b); Jackson Co., FL (Loomis 1943); and Mobile Co., AL (Causey 1954).

E. simplex Chamberlin 1920. Reputedly New Orleans, Orleans Par., LA, but probably some 145 miles to the west northwest around Evangeline and Rapides parishes.

E. birdi Chamberlin 1931. Unspecified site in Murray Co., OK. Also reported from Seminole, Pittsburg, and Hughes cos., OK, and Sebastian, Logan, and Miller cos., AR (Causey 1952b); and Red River and Lamar cos., TX (Stewart 1969).

E. mundus Chamberlin 1931. University (of Oklahoma), Norman, Cleveland Co., OK. Also recorded from the Wichita National Forest, now National Wildlife Refuge, Comanche Co., OK (Chamberlin 1931); and Latimer, Caddo, and McClain cos., OK, and Sevier Co., AR (Causey 1952b).

E. melacis Chamberlin and Mulaik 1941. Type locality not specified in description, and two samples are labeled "holotype": a female from Raven Ranch, Kerr Co., TX, the first site listed in the account and which was recorded as the type locality by Chamberlin and Hoffman (1958), and a male from Edinburgh, Hidalgo Co., TX. Also reported from Kendall, Bandera, and Concho cos., TX (Chamberlin and Mulaik 1941); Uvalde Co. (Chamberlin 1952); Comal and Guadalupe cos. (Loomis 1959); and caves in Bexar, Kerr, and Uvalde cos. (Reddell 1970).

E. newtonus Chamberlin 1942a. 1.2 mi. S Jasper, Newton Co., AR.

E. oliphantus Chamberlin 1942a. 15 mi. SW Oliphant, Jackson Co., AR.

E. creolus Chamberlin 1942a. 5 mi. NW Shreveport, Caddo Par., LA.

E. louisianae Chamberlin 1942a. 2 mi. S Saline, Natchitoches Par., LA.

E. schmidti Chamberlin 1943 (=*E. plishneri* Causey 1950a). Rich Mtn., Polk Co., AR. Also recorded from Carroll and Washington cos., AR (Causey 1950a); and Franklin and Benton cos., AR (Causey 1952b).

E. dubius Chamberlin 1943. Delight, Pike Co., AR. Also reported from Clark, Dallas, Hot Springs, Saline, and Sevier cos., AR (Causey 1952b).

E. christianus Chamberlin 1946 (=*E. spectabilis* Causey 1950a). Pass Christian, Harrison Co., MS. Also cited from Columbia Co., AR (Causey 1950a); Union Co., AR, and Claiborne Par., LA (Causey 1952b); and Washington and East Baton Rouge Pars., LA, Mobile Co., AL, and Jackson Co., MS, (Causey 1963).

E. bentonus Causey 1950a. Monte Ne, Benton Co., AR. Also recorded from Carroll Co., AR (Causey 1950a).

E. planus Causey 1950b. Piney Woods, Rankin Co., MS.

E. angularis Causey 1951. DeValls Bluff, Prairie Co., AR.

E. compressus Causey 1952a. Junction City, Union Co., AR.

E. wellesleybentoni Causey 1952a. Helena, Phillips Co., AR.

E. sanbernardiensis Causey 1952a. San Bernard River at US hwy. 59, Fort Bend Co., TX.

E. goodi Causey 1952b. 16 mi. S Mena, Polk Co., AR.

E. amplus Causey 1952b. Ruston, Lincoln Par., LA.

E. hamatilis Loomis 1969. 8 mi. N Zavalla, Angelina Co., TX.

E. digitatus Loomis 1976. 5 mi. ESE Marble Falls, Burnet Co., TX.

Genus **Paresmus** Chamberlin 1942a.

P. impurus (Wood 1867). Long Point, near Brenham, Washington Co., TX.

P. paroicus Chamberlin 1942a. 1.5 mi. N Clay, Lincoln/Jackson Pars., LA.

P. pulaski Causey 1950a. 3 mi. S Sweet Home, Pulaski Co., AR. Also recorded from Sheridan Co., AR (Causey 1952b), and Grant Co., AR (Chamberlin and Hoffman 1958).

P. columbus Causey 1950a. 3 mi. E Magnolia, Columbia Co., AR.

P. polkensis Causey 1952b. 11 mi. N Mena, Polk Co., AR.

Anatomy and Taxonomic Characters

A family level revision is a formidable challenge, and particularly in the Eurymerodesmidae, where none of the nominal species has been characterized in accordance with modern standards and the taxonomically important characters are unknown. Nor has anyone searched for logical patterns in the different aperture types, which promise to be very useful in making determinations. Species distributions are also unknown, so geographic data cannot facilitate identifications. Finally, the higher taxa are very poorly defined. Distinctions between the genera are unclear, and although Causey (1951) listed some autapomorphies of the family, their taxonomic utilities at either the generic or specific levels have not been investigated. The more than 40 publications dealing in part with eurymerodesmids are useless for revisionary purposes, since they consist chiefly of either terse and unreliable locality references or mere validation statements for scientific names. This situation is much worse than that of the Xystodesmidae in 1974 when I began studying that family; several genera had been revised, and the literature was reasonably advanced. Nothing definitive has been published on the Eurymerodesmidae, so my task as first reviser is to fill as many voids as possible, realizing that some will remain because of the impoverished initial level of knowledge. Thus, I first examined the available type specimens to ascetain the forms in question, since most illustrations are meaningless, uninterpretable sketches. Next came the reservoir of unstudied and unidentified material in institutional collections that, as expected, contained new forms and the answers to taxonomic questions, particularly which characters hold diagnostic utility. Because it was impossible to thoroughly investigate every potentially useful character, I review general eurymerodesmid external anatomy in this section as well as features found to be taxonomically important. Development of other potentially important characters is left to future workers.

At the outset it is informative to digress and review the historical development of taxonomic characters *per se*. Only two of the diagnostic autapomorphies were known before family status was proposed in 1951, and only one was recorded before 1943. Despite the elaborately ornamented apertures, the hairs on the prefemoral stem were the only unique feature observed by early authors. Wood (1864, 1865) noted them in the original descriptions of *hispidipes,* stating that the male genital appendages were "beset with very numerous long hairs," which are shown extending to the tip of the telopodite in his illustration (1865, fig. 48). Although the account is internally contradictory, Wood (1867) also mentioned the hairs in the description of *impurus*. McNeill (1887) did not allude to hairs in the description of *varius* because the types were females, but Brolemann (1900) used them along with the absence of a "secondary ramus," or prefemoral process, as justification for proposing *Eurymerodesmus* as a new subgenus of *Fontaria*. He provided an illustration of *amplus,* the Louisiana species that he (Brolemann 1895) recorded as *hispidipes,* and noted the presence of a row of long silken hairs along the length of the seminal branch almost to its tip. Curiously, in elevating *Eurymerodesmus* to generic status fifteen years later, Brolemann (1915) ignored the hairs, giving as his criteria a large femur supporting a short, slightly bent seminal branch without an apical opening, and adding that the secondary branch was absent. In a brief generic account and 11 subsequent species descriptions, Chamberlin (1920, 1931, 1942a, 1943)

and Chamberlin and Mulaik (1941) continued to mention the prefemoral hairs but did not cite any other autapomorphies, although Chamberlin (1931) did report and illustrate the lobes of *birdi* and *mundus*. Consequently, Loomis (1943) became the first author to note another feature when he mentioned in the description of *minimus,* a synonym of *v. varius,* that the mandibular stipes ended simply rather than in an "incurved process" as in males of *mundus* from Dallas County, Texas. This statement apparently did not register with Chamberlin (1946), as he said nothing about the mandible in the description of *christianus*. Thus, the recognition of the uniqueness of *Eurymerodesmus* must be attributed to Causey (1950a), who noted in a brief generic account that the gonopodal opening was variously modified posteriorly and laterally with setose lobes, that the telopodite was a "single, unbranched, slender blade with setae usually in rows," and that the leg femora, presumably meaning prefemora, were unspined. She did not include the mandibular projection in the generic account but characterized and/or illustrated it and the second leg coxa in all six descriptions that year (Causey 1950a, b). The following year, Causey (1951) erected the family and listed most of the autapomorphous features, which she characterized in the six species proposed the next year (Causey 1952a, b). Thus, 79 years elapsed from the date of the first species until a second family character was recognized, and seven more passed before other unique features were recorded. Only 87 years later was *Eurymerodesmus* properly assigned to a separate family. The prefemoral hairs have always been associated with *Eurymerodesmus,* but the other diagnostic characters have only been recognized in the past three to four decades. Developing these as fully as possible is a major objective of this work.

Body size. — Individual body size is a subjective criterion at best, and particularly in the Eurymerodesmidae because of the brittleness and rigidity of most preserved specimens. Females are generally larger and more vaulted than males, but both sexes tend to fragment or even shatter with handling. One should therefore measure the length while the animal is alive or freshly killed, a task for future workers since this study is based primarily on preserved specimens. Most eurymerodesmids that I encountered alive were tightly coiled under leaves or in upper soil layers. They die and are preserved in this posture, and hence must be uncoiled for measurement and examination of the genitalia. They usually fragment during this process beyond the state where they can be reassembled for reasonably accurate length measurements, although large species tend to be more flexible than small ones. However, despite the difficulty in measuring lengths, some species are so obviously larger or smaller than others that size alone is a clue to identity, even in the field, although it should always be confirmed by examining the genitalia. For example, because *varius* is so much shorter, one could usually distinguish it from such sympatric species as *birdi* and *angularis* in Mississippi and southeastern Louisiana. Likewise in Texas, the components of the *melacis* lineage are generally smaller than parapatric or sympatric forms of *birdi* and *amplus*. Conversely in southern Arkansas and northern Louisiana, *angularis, compressus, goodi, dubius,* and *polkensis,* the largest eurymerodesmids, stand out in contrast to such smaller species as *birdi, mundus,* and *amplus*. Averaging all measurements of each species, I propose the following general size or length categories, to be modified by measurements of fresh material. They are useful when forms at opposing extremes, such as small or small to moderate and large, are found sympatrically.

Table 1. Size Categories for Species and Subspecies of *Eurymerodesmus*.

Category	Length (mm)	Species
Small	under 18.0	*v. varius, varius christianus, varius* intergrades, *melacis, clavatus.*
Small to Moderate	ca. 19-23	*hispidipes, varius louisianae, oliphantus, elevatus, dactylocyphus, sanbernardiensis, digitatus.*
Moderate	ca. 25-30	*impurus, amplus, newtonus, simplex, caesariatus, birdi, mundus.*
Moderately Large	ca. 30-32	*paroicus, crassatus, pulaski, serratus.*
Large	above 32	*angularis, compressus, goodi, dubius, polkensis.*

Head. — The head of eurymerodesmids, which is smooth and glossy with few facial setae, can easily be mistaken for that of a xystodesmid. The epicranial suture is distinct, bifid, and terminates in the interantennal region. The epicranial and interantennal setal series are usually absent; subantennal setae, one per side, are usually present; and when present, frontal and genal setae are few in number. The genae may or may not have faint central impressions, and the ends are rounded and extend beyond the adjacent cranial margins. As in xystodesmids, the antennae are long and slender, becoming progressively more hirsute distally, with antennomeres

2-6 being clavate. The four terminal cones are the only apparent sensory structures.

Projection of the mandibular stipes. — In both sexes the mandibular stipes possesses a mid-ventral ridge that becomes broader distad, extending beyond the corner of the stipes into a medially directed process. The projection is distinct and extends well beyond the stipes in most males, whereas it is a rounded indistinct vestige in nearly all females. The projection in males may have more taxonomic utility than currently realized, and future workers may devise a quantifying index for identifications. Obvious differences in length, breadth, degree of sclerotization, apical configuration, and whether it is linear or bowed are potentially useful, but I can only note them and characterize the structure for descriptions. However, the nubbinlike projection in males of *v. varius, varius christianus,* and *varius* intergrades, which resembles the minute projections of females, is so much shorter as to be diagnostic for these forms. Combined with size, this structure distinguishes these forms of *varius* without examining the gonopods or apertures, but unlike other eurymerodesmids, their sexes cannot be recognized by the size and shape of the process. The other subspecies, *varius louisianae,* cannot be distinguished unerringly from sympatric congeners because its process is longer, broader, and more typically male-like. Since the projection is short and subtriangular in *clavatus,* it may also distinguish this Texas species from sympatric or parapatric congeners. However, more material is needed of *clavatus,* known only from the type locality, before this can be stated with confidence.

Terga. — The dorsum of eurymerodesmids closely resembles those of xystodesmids, and the two families have been confused on several occasions probably because of the triangular epiprocts and generally parallel-sided segments that taper slightly caudad. The collum is considerably broader than the succeeding terga but does not always extend below them (Fig. 89). The anterior surfaces of the paranota are excavated below the anterior corners, which are broadly rounded on all segments thus distinguishing eurymerodesmids from platyrhacids, with which they are also confused as evidenced by Chamberlin's proposal (1942a) of *booneus* for juveniles of *Auturus evides.* American platyrhacids have body dimensions similar to moderate-size eurymerodesmids, but they have a broad, truncate epiproct and small but distinct teeth on the anterior paranotal corners, which are less rounded than those of eurymerodesmids. The teeth and truncate epiproct are clearly visible on juvenile platyrhacids like the types of *booneus* and even early instars, so these two features invariably distinguish the two families. To separate eurymerodesmids and xystodesmids, one must examine the mandibles, the legs, the pregonopodal sternal projections, or the genitalia of both sexes.

Sterna. — The projections of the sterna in male eurymerodesmids may also possess taxonomic utility, a decision left to future workers. In contrast to xystodesmids, the sterna of male eurymerodesmids are extremely hairy, particularly those on pregonopodal segments. Eurymerodesmids lack a projection on segment 4, but segments 5-6 display a variety of elevations ranging from broad flattened areas to moderately long knob-like projections, all shorter than the adjacent coxal widths and apically hirsute. Likewise between the 9th legs,[1] there are a variety of apically setose elevations and knobs, which coalesce medially in some forms of *dubius* (Figs. 49-51) into a single large projection that can be longer than the adjacent coxal widths (Fig. 50). The remaining sterna become progressively flatter posteriorly with progressively sparser hair patches subtending the coxae. This is also the condition in females, which generally lack sternal projections and have at most only slight elevations on the anteriormost segments.

Legs. — Eurymerodesmid legs are subsimilar in size on all segments of both sexes; none are reduced or crassate. In addition to short, cylindrical, and truncate gonapophyses, the 2nd coxae of males exhibit variable distal lobes at the anterior and/or caudal margins, with the former usually being larger (Fig. 3). Otherwise the legs lack ventral spines and tubercles, and eurymerodesmids can thus be distinguished from sympatric xystodesmids by the absence of the ventrodistal prefemoral spines characteristic of the latter. However, the prefemora of males do have large rounded lobes on the dorsal surfaces (Fig. 4), which differ in size between species and extend caudad for varying numbers of segments. In *angularis, compressus, goodi,* and *crassatus* the lobes extend nearly to the caudalmost legs, although diminishing caudal to midlength, whereas in *clavatus, digitatus, simplex,* and *varius,* they are restricted to the anterior half of the body, the pregonopodal segments on the last species. In the other

[1] The gonopods in polydesmoids, located at the anterior position of segment 7, represent the highly modified 8th legs. I therefore refer to the posterior legs on segment 7, the first postgonopodal pair, as the 9th legs even though they are technically the 8th ambulatory appendages in adult males.

eurymerodesmids, the prefemoral lobes terminate from segments 10-16, 10-12 on most species. Female eurymerodesmids and both sexes of xystodesmids lack these lobes. Eurymerodesmid tarsal claws are slightly hooked, with a hint of bisinuate curvature in some species, and arise from a thickened, globose basal mass.

Male genitalia. — Although the female cyphopods distinguish *compressus, dactylocyphus,* and some forms of *amplus* and *angularis,* most of the specific characters in *Eurymerodesmus* involve aspects of the male genitalia, which in this family refers collectively to both the aperture and gonopods.

1. *Aperture.* — The configuration of the aperture, elaborately ornamented in some species, is the most obvious characteristic of the Eurymerodesmidae. Features such as the caudolateral pouches of *oliphantus, paroicus, angularis,* and some forms of *amplus,* and the lobes of *mundus* and the westernmost population of *b. birdi,* are so striking as to compel attention to their taxonomic utility and function. Aside from *hispidipes,* in which the aperture is uniformly elevated, it is hard to understand how early workers could have overlooked them. Conversely, the gonopods at first glance appear so uniform as to be virtually devoid of information, but detailed study reveals that they contain subtle taxonomic characters in contrast to the obvious features of the apertures. Thus, eurymerodesmid determinations rely chiefly on a combination of gonopodal and aperture characters.

Ironically, the intricacies of the apertures hampered revision because there are no applicable precedents. To my knowledge they are unique in the Chelodesmidea, and perhaps also in the order Polydesmida, and therefore require a new format and terminology. After pondering how to verbally portray the opening, I decided to detail sequentially the anterior, anterolateral, lateral, caudolateral, and caudal margins. In addition to structural details, they also vary in the degree of hirsuteness, which in some forms is almost as striking as the marginal configurations. Consequently, the aperture descriptions in the species accounts adhere to the following format: a) an overview of the aperture describing its basic type, the general configuration of the opening itself, width and length measurements, and if different from the opening, the general shape of the entire aperture including marginal adornments; b) the sequential description of the anterior margin, sides, caudolateral corner(s), and caudal margin; and c) a characterization of the aperture hairs in the same sequence. I recognize two basic types of apertures, with and without divided lateral margins and caudolateral pouches. The latter category is further divided into forms with or without lobes projecting above the general marginal elevations and located from the caudolateral corner and the adjoining part of the sides to near midlength of the caudal margin. The species displaying these aperture conditions are listed in table 2. Two general areas are circumscribed in forms with caudolateral pouches — that of the opening itself, and that of the opening plus the folds, flares, and marginal adornments, referred to as the "aperture apparatus." Both types of apertures possess indentations at the midline of the anterior margin, and both extend anteriad in the metazonum, thereby compressing the prozonum into a narrow band. This is most apparent by comparing the stricture lines in ambulatory and gonopodal segments, as shown in figures 5-6 for *hispidipes.* On midbody segments, the stricture curves smoothly and bisinuately, but on the reproductive segment, it angles anteriad laterally, disappears near the anterolateral corner, and reappears as a short, curved, basal line on the anterior indentation. Hoffman (1979) stated that the apertures in both eurymerodesmids and holistophallids protrude into the prozonum, but my examinations show that this region is compressed in the Eurymerodesmidae. I have never been able to trace the stricture completely, but it is particularly well defined in a few

TABLE 2. Aperture conditions in *Eurymerodesmus.*

Sides divided, with pouches	Sides entire, without pouches	
	With lobes	Without lobes
angularis	*polkensis*	*hispidipes*
compressus	*serratus*	*impurus*
varius	*birdi birdi*	*goodi*
amplus	*mundus*	*dubius*
newtonus		*caesariatus*
oliphantus		*pulaski*
elevatus		*birdi planus*
simplex		*melacis*
paroicus		*dactylocyphus*
crassatus		*sanbernardiensis*
		digitatus
		clavatus

males and can be followed around the anterolateral corners to almost join the line on the anterior indention. The broadest aperture occurs in *dactylocyphus,* where it fills the segment width in ventral view (Fig. 184), and in a few individuals the aperture extends so far anteriad that the prozonum is reduced to a narrow sliver, the minimum necessary to maintain structural integrity of the

segment. The stricture is invisible on the anterior indentation in these males, but its greater angle laterally further suggests that the prozonum is compressed rather than penetrated.

a) Anterior margin. — In every species except *dactylocyphus,* where it is elevated into a narrow rim that curves around the anterolateral corners, the anterior margin is flush with the metazonal surface. All species except *caesariatus* possess a midline indentation that varies in length and breadth, and may be apically rounded to acute. In *goodi, polkensis, paroicus, crassatus, pulaski, serratus,* and *sanbernardiensis* it is a long, distinct projection, extending well into the opening proper (Figs. 39, 114, 123, 127, 134, 142, 191); the opposite extreme occurs in some forms of *dubius, varius,* and *b. birdi,* where it is slight and barely detectable (Figs. 50-51, 56, 154).

b) Anterolateral corner. — The anterolateral corner, broadly rounded, poorly defined, and subsimilar in nearly all species, is more abstract than real, but is nevertheless a convenient reference point for the origins of the sides or lateral margins. Except for *dactylocyphus,* where it is elevated, the corner is flush with the metazonal surface in all species, at least on the anterior part of the curvature. The lateral elevations begin near the corner in many species, rising so close in some that they can truly be said to originate there. Since this corner is unadorned in eurymerodesmids, it is omitted from the species descriptions.

c) Lateral margins. — The sides or lateral margins are the most variable and complex parts of the aperture. There are two basic types — divided, and undivided or entire — and the elevations begin at varying distances behind the anterolateral corner in both. In undivided forms the elevation usually continues rising to the caudolateral corner, where it can terminate as in some forms of *dubius* (Fig. 46), continue around the corner onto the caudal margin as in *hispidipes* (Fig. 6), or continue caudad, tapering to the metazonum behind the corner as in *impurus* (Fig. 11). The rate of elevation varies from uniformly flattened as in *hispidipes* (Fig. 6), to gradual as in *digitatus, sanbernardiensis,* and *clavatus* (Figs. 191, 198, 205), to steep as in *impurus* (Fig. 11). The elevation may also be upright as in *hispidipes* or lean slightly mediad, thus narrowing the opening, as in *serratus* and some forms of *b. birdi* (Figs. 142, 149).

In the type population of *birdi planus,* the sides are essentially flush with the metazonum throughout their lengths (Fig. 162), and they angle caudomediad forming a heart-shaped opening in conjunction with the anterior indentation. Thus in undivided species, the angle of the sides varies from the condition in *b. planus* to nearly linear as in *hispidipes* (Fig. 6), to multiangular as in *dactylocyphus* (Fig. 184). In undivided forms the configuration of the apparatus and the opening are the same, and hence the former is omitted from species descriptions. Variation obtains in the angle or direction of the sides and the rate and lean of the elevation. The elevations, particularly slight ones, are difficult to show from above in line drawings, some of which are close approximations of the actual condition.

In species with divided lateral margins, the configuration of the apparatus usually differs from that of the opening itself; consequently, both are characterized in descriptions. The divisions occur in the caudal halves of the sides, the anterior halves resembling the condition in undivided species, with a variable elevation, which may be upright or lean over the opening. At the division point, usually the highest part of the side, the margin divides into two lateral margins that continue around the caudolateral corners to form two caudal margins. In most species the division point is clearly visible in ventral view, and the "inner lateral margin" angles into the opening, curves through the "inner caudolateral corner," and blends into the "inner caudal margin." The more variable "outer lateral margin" can continue the upward slope of the anterior part of the sides as in *elevatus* (Fig. 97), descend to a lower level as in some forms of *angularis, varius,* and *newtonus* (Figs. 21, 56, 84), or flare or angle sublaterad to varying degrees, in some species extending well beyond the level of the stigmata, as in *oliphantus* and some forms of *amplus* (Figs. 78, 91). The "outer caudolateral corner" is more distinct than its inner counterpart and connects with the "outer caudal margin." Up to division point the rim varies from essentially smooth to slightly irregular. After division point, the inner lateral margin is always smooth, but the outer lateral margin can be as variable as the undivided part of the sides.

d) Caudolateral corners. — The caudolateral corner, in many species imperceptible and poorly defined, is the reference point separating the sides and caudal margin; there are inner and outer corners in forms with divided sides. The inner caudolateral corner is almost always a smoothly rounded blending of the inner lateral and caudal margins. The outer corner, however, varies from sharp as in some forms of *amplus* and *oliphantus* (Figs. 77-78, 91), to blunt in

some forms of *angularis* and *amplus* (Figs. 18, 21, 76), to poorly defined as in *newtonus* (Fig. 84). It is usually elevated above the metazonal surface, merging with the latter a short distance along the outer caudal margin. The outer and inner lateral margins are separated to varying degrees, forming a "pouch" or cavity between them at the caudolateral corner. The cavity likewise varies in breadth, depth, and the degree to which it is open or closed, or obscured in ventral view, in turn reflecting the degree of lean in the outer lateral margin. For example, the pouch in *varius* is closed (Figs. 56, 64, 68), whereas that in *olilphantus* is open (Fig. 91), and the outer lateral margin angles strongly sublaterad to form the broadest pouch in the genus, with the inner margin visible throughout its length. The pouch in the variant of *amplus* named *hamatilis* by Loomis (1969) (Fig. 78) is slightly less open than that of *oliphantus*. Forms with broadly open caudolateral pouches often exhibit bizarre configurations of the aperature apparatus, for example trapezoidal in some forms of *varius* and *oliphantus* (Figs. 59, 91), while the actual opening is broadly ovoid.

Thus, the caudolateral pouch is the cavity between the outer and inner margins at the caudolateral corner; it usually gives rise to variable tufts of short hairs. In most species, the two margins form the inner and outer boundaries of the cavity, and this condition is termed a "true pouch." Both *elevatus* and *impurus,* divided and undivided species, respectively, display a different pouch (Figs. 11, 97), in which the lateral elevations continue to rise caudally, and the inner surfaces are cupped and give rise to hairs. These are not true pouches because the cavity is primarily on the inner surface of the outer margin. The inner lateral margin of *elevatus* and the caudal part of the lateral margin in *impurus* form the base of the cavity rather than its inner boundary. Consequently, these pouches are anatomically different and are termed "false pouches."

The caudolateral corner in undivided species varies as in divided ones. The only other noteworthy point is that the lobe is located there in some forms of *b. birdi.*

e) Caudal margin. — In divided species, the caudal margins are essentially parallel and do not display striking modifications. Occasionally the outer or both margins may angle slightly caudad in the midline, even merging with the sternal projection(s) between the 9th legs as in some forms of *dubius* (Figs. 49-50). The outer caudolateral corner may be slightly elevated, but the outer caudal margin drops rapidly to the metazonal surface. The caudal margin is more variable in undivided forms, particularly *b. birdi* and *mundus,* where extremely long lobes extend above the general marginal elevation, the locations varying from the caudolateral corner to near midline of the caudal margin. In *mundus* and the westernmost population of *b. birdi* these lobes project well below the adjacent coxal margins (Figs. 149-150, 169-170), and similar but smaller lobes occur in *polkensis, pulaski,* and *serratus.* The clavate lobes of *mundus* (Figs. 169-171) are always well removed from the caudolateral corner and located about 1/3 of the distance along the caudal margin. The broadly subtriangular lobes of *b. birdi* can occur from the caudolateral corner and adjacent part of the sides to well along the caudal margin. As seen in caudal profile, they can be in alignment with the succeeding sternal lobes (Fig. 151) or lateral to these (Fig. 156). Another undivided species with a striking feature at the caudolateral corner and caudal margin is *dactylocyphus.* Here the sides begin to rise near midlength, accelerate and extend well ventrad near the caudolateral corner, and expand onto the caudal margin. This structure is more of a cupped flange than a lobe, and hairs arise from the concave inner surface.

f) Aperture hairs. — Aperture hairs are highly variable throughout *Eurymerodesmus.* In forms like *b. planus, digitatus,* and *clavatus* (Figs. 162, 164, 168, 198, 205), hairs occur chiefly at the caudolateral corner and adjacent parts of the sides and caudal margin. In *goodi,* hairs arise at the anterolateral corner and continue onto the caudal margin (Fig. 39), while in *angularis, compressus, oliphantus, simplex, paroicus, crassatus, b. birdi, mundus,* and *melacis,* the anterior margin is covered to varying degrees (Figs. 18, 32, 91, 103, 123, 127, 149, 154, 169, 178). Hairs tend to be somewhat thicker on the sides of the anterior indentation, then they taper off and occur sporadically or regularly along the anterolateral corners and anterior parts of the sides, arising both from the rims and from the outer surfaces of the sides. Densities tend to increase at or near the caudolateral corners, with tufts in the pouches coming from either the under surfaces of the outer lateral margins or from the pouches proper. In some forms of *angularis* and *varius,* the division point extends inward into the opening before dividing into inner and outer margins, and often there will be a hair tuft under this extended division point (Figs. 23, 59). On undivided species without lobes, the hair pattern tapers off on the caudal margins with at most only a few scattered hairs, usually arranged linearly. However, the lobes of *mundus* and *b. birdi* are so

densely pilose, that the surface is obliterated. Hairs begin basally, become denser and longer distad, and are directed distad. In some populations of the latter with moderate-size lobes, the distal hairs are as long as the lobes themselves (Fig. 155).

2. *Gonopods.* — Eurymerodesmid gonopods are undivided, linear to gently curved structures without a solenomerite or prefemoral process, and feature long hairs that extend distad along the prefemoral stem. They are oriented laterally *in situ* with the cannula on the lateral rather than the medial side as in other chelodesmoids, and the telopodites project caudad from the aperture instead of anteriad as in other chelodesmoids. The condition in the Eurymerodesmidae therefore represents a 180° rotation in that both the cannula and telopodite have moved to opposite sides of the aperture; the coxa is also twisted so that the cannula is exposed *in situ* instead of being only slightly visible on the side of the coxa. In eurymerodesmids, the telopodites overhang and extend beyond the caudal aperture margin(s) (Figs. 6, 11, 21, 59, etc.), in many overlapping the 9th coxae or the intervening sternum. However, this also partly reflects compression of the body segments; occasionally, the anterior segments are so tightly coiled that the telopodites overhang segment 8. In *dactylocyphus, goodi,* and a few other species, especially those in the *melacis* lineage, the telopodites terminate before the caudal margin and are wholly enclosed by the aperture (Figs. 39, 184, 191, 205), a condition caused by a very broad aperture and short telopodites. The only exception to the caudal orientation is *caesariatus* (Fig. 117), in which the short telopodites extend directly ventrad, although in a two dimensional drawing they appear to be directed anteriad.

In situ configurations vary from parallel and narrowly to widely separated (Figs. 18,32, 91, 123, 127), to overlapping in the midline (Figs. 21, 59, 73, 76, 149). These arrangements seem to have little taxonomic utility, but *paroicus* and *crassatus,* with the broadest, heaviest telopodites, are the most widely segregated. Telopodite apices are directed variably laterad to dorsad and are sometimes obscured by more proximal parts of the structure.

a) Coxae. — The coxae have no taxonomically significant features as far as I can determine. They are loosely joined by membrane with no trace of a sternal remnant and in fact are loosely held in the aperture on all sides. The membrane holding them in place tears easily, with that between the coxae being thicker and tougher. Thus to remove a single gonopod, I recommend tearing the intercoxal membrane first while the structures are still attached to the inside of the aperture.

The coxae are large and globular, lack apophyses, have a single macroseta on the dorsal surface below the base of the cannula, hence invisible *in situ,* and carry a short, broad sternal apodeme. Their lateral orientation, representing a 180° rotation from the condition in the rest of the suborder, is an important autapomorphy for the family, and the coxa has also been twisted to bring the cannula to the open or ventral surface. The unpaired macroseta constitutes another difference from the Xystodesmidae, where there are two paired marcosetae per coxa. The term, macroseta, applies to the Xystodesmidae, where it is longer and stouter than the hairs on the base of the prefemur, but it is actually a misnomer in the Eurymerodesmidae because the seta is subsimilar to the larger ones on the prefemur. However, since it carries no taxonomic value, there is no reason to coin a new term.

b) Telopodite. — In the ensuing descriptions, I treat the prefemur and acropodite separately, saying little about the telopodite, which contains little taxonomic information. However, the telopodites do vary greatly in length, from the short ones of the *melacis* lineage to the long ones of the *birdi* lineage. The telopodites may be essentially linear, with at most only a slight curve on the acropodite or the distal extremity of the prefemur (Figs. 47, 199), or it may curve or lean to varying degrees over the coxa (Fig. 185). It may terminate short of (Figs. 47, 86, 93, 111), or at (Figs. 98, 124) the level of the distal extremities of the hairs. In most species the prefemur comprises as much as 7/8 of the length of the telopodite (Figs. 8, 47, 119, 172, 179), but in the *impurus* group, the prefemur is much shorter, constituting from 1/2 to 3/4 of the telopodite length (Figs. 12, 24, 40). In *paroicus, crassatus, pulaski,* and *serratus,* which have subterminal acropodites, the prefemur comprises the entire length of the telopodite.

c) Prefemur. — The prefemur arises centrally on the ventral surface of the coxa and consists of two parts — a broad basal mass, closely appressed to, and partly submerged in, the coxa, and the distal stem, which is directed caudoventrad to ventrad. The basal mass extends mediad along the coxa, bending abruptly ventrad just before the medial coxal margin, which therefore extends beyond the bend as seen in lateral profile of some species (Figs. 69, 85, 92, 98). The basal mass is invested with long matted hairs that are half as long as the prefemoral stem in many species and are so dense that they

obscure the shape of the mass itself. The latter appears as a silhouette through the hairs, its exact boundary uncertain. The basal hairs also obscure the proximal part of the prefemoral stem in lateral view, so for drawings from this perspective one must extrapolate lines from the visible, distal part of the prefemur.

The prefemur can be of subequal width throughout, with sides roughly parallel, or it can taper or expand distad. The last condition occurs in *simplex* and *clavatus* (Figs. 104-105, 206-207), in which the prefemur expands distal to midlength into broad shoulders on the outer and inner margins, respectively. *Eurymerodesmus varius* contains intermediate forms with strong distal lobes on the outer surfaces in *v. christianus* (Fig. 65), intergrade populations with small lobes at this position (Fig. 63), and forms without a trace of a swelling, represented by some populations of the nominate subspecies (Figs. 57-58). No precursor forms are known for the clavate condition on the inner surface shown by *clavatus*.

The most striking characteristic of the prefemoral stem is the long hairs along the inner surface, a continuation of those on the basal mass. They are the only autapomorphy of the family to have been observed by early authors and have long been used to distinguish *Eurymerodesmus*. The hairs are of several different lengths and breadths, a distinction that may also possess taxonomic utility. The most conspicuous hairs on the prefemoral stem are long and broad, and I like Brolemann's characterization (1900) of long, silken hairs. Some species, for example *serratus* (Fig. 145) also display shorter, denser hairs on the stem. The broadest hairs occur in the corona of *caesariatus* (Figs. 118-119), where they are packed so tightly as to appear sclerotized. The hairs extend, usually in two rows, along the inner prefemoral surface for most of its length, or to the level of the acropodite when this structure is subterminal, thereby marking the course of the prostatic groove. In all species except *varius,* the hairs are relatively continuous and regularly arranged, with only occasional small gaps. In *varius,* however, they are sparse and sporadic (Figs. 57-58, 63, 65, 69-71). All species also have a variable tuft on the outer or medial margin at the distal extremity of the prefemur, distal to the inner hairs. The density of this distomedial tuft, the number of hairs, and the length it extends proximad vary. Some species also have two or three scattered hairs proximal to this tuft on the outer surface, occasionally extending to the basal prefemoral bend.

d) Acropodite. — In most species of *Eurymerodesmus,* the acropodite is very short, only about 1/4 to 1/8 of the total telopodite length. However, as the prefemur becomes shorter in the *impurus* group, the acropodite becomes correspondingly longer, constituting 1/2 to 3/4 of the length of the telopodite (Figs. 12-13, 19-20, 22, 24, 33-34, 40-41). The position and basal breadth of the acropodite are also taxonomically important. It is broadly terminal in most species, its basal width being essentially the same as the distal width of the prefemur, so that the structures blend smoothly together with an indistinct juncture. Such acropodites are described as smoothly continuous with, and poorly demarcated from, the prefemur (Fig. 47). In *varius christianus,* the acropodite is broadly terminal, but is sharply demarcated from the prefemur because of the latter's distal lobe (Fig. 65). In *simplex, polkensis,* and *caesariatus,* the acropodite is narrowly terminal, arising solely from the inner prefemoral margin. The outer margin terminates bluntly in *polkensis* and *caesariatus* (Figs. 111-113, 115, 118-119), and expands into a shoulder in *simplex* (Figs. 104-105). *Eurymerodesmus clavatus* is the obverse in that the narrowly terminal acropodite arises from the outer prefemoral margin with the inner surface expanded into a shoulder (Figs. 206-207). Finally, there are four species in which the acropodite is subterminal and arises from the inner margin of the prefemur at varying distances from the tip — *paroicus, crassatus, pulaski,* and *serratus.* These species demonstrate the most bizarre, apomorphic gonopods in the family, because the acropodite is also usually short, and the prefemur displays modified margins with irregularities, serrations, and/or concavities. In *pulaski* and *serratus,* the acropodite arises in a cavity on the inner prefemoral surface, which expands into a hood shielding the structure. In *pulaski* the expansion is long and narrow (Figs. 135-136, 138), but in *serratus* it is short and broad, with an intricately serrated margin (Figs. 143-145). The acropodite in *pulaski* is little more than a thickened boss, but it is longer in *serratus,* and the combined effect with the expanded hood resembles the distal configurations in the xystodesmids *Sigmoria (Cheiropus) planca* (Loomis) and *S. (C.) serrata* (Shelley) (see Shelley 1984b). Consequently, the acropodite varies from broadly terminal and poorly demarcated from the prefemur, to broadly terminal and sharply demarcated, to narrowly terminal, to subterminal. These traits and its length confer more taxonomic utility on the acropodite than the prefemur, and one's initial

observations of a eurymerodesmid should be of the acropodite and aperture. Even in broadly continuous, poorly demarcated forms, the configuration of the aperture is vitally important in distinguishing between such species as *newtonus* and *amplus,* and *melacis* and *digitatus.* The principle distinction between the first pair is the uncinate acropodite of *newtonus* (Figs. 85-86). Likewise, the acropodite bends sharply laterad from the prefemur in *melacis,* whereas it curves broadly dorsad in *digitatus* (compare Figs. 178-180 and 198-200).

In all species, the prostatic groove runs along the inner surface of the prefemur onto the acropodite and opens terminally.

Female genitalia. — In contrast to the Xystodesmidae, female cyphopods display several taxonomically important features. Some features allow accurate assignment to species, whereas others allow placement in a species group. Beyond the cyphopods themselves, the apertures display elevations, flares, and other marginal modifications that may also have taxonomic utility, even though they are not as spectacular as those of males. I did not thoroughly examine female apertures, and investigations of this structure are left to future workers.

The cyphopods display the basic chelodesmoid form, with two variably hirsute valves, open basally and joined distad, attached to a glabrous receptacle on the closed, usually lateral, side, with a much smaller, densely hirsute operculum basally. The *in situ* position of the cyphopods varies from transverse (Fig. 114), to along the body axis (Figs. 42, 201), to oblique (Fig. 35), and may also have taxonomic importance. Eurymerodesmid cyphopods are comparatively large, and in relation to body size are proportionally much larger than those of eastern xystodesmids. Their various parts are also proportionally large, particularly the receptacle and operculum. The latter lacks taxonomic significance, but is oblong in profile, wider centrally in head-on view, and gives rise to long curved hairs from its outer surface. Although the operculum is the smallest component of the cyphopods, it is not so minute as to be practically invisible. It is always evident in front or head-on view, and except for species in which the receptacle curves partly around it, the operculum is also clearly visible in profile.

1. *Valves.* — The valves are the dominant feature of the cyphopods, the most visible structures *in situ* and larger than the other parts combined. They are highly variable, equal or unequal in size, and the open surface is variably hirsute. The joined distal margin is elevated in many species, diagnostically so in a few. In species like *varius,* the elevation is insignificant (Fig. 61), but in others it extends into a distinct rim that protrudes through the aperture. Such a rim is displayed by *amplus,* in which it varies from linear, to angled toward the distal corner, to angled with a short terminal papilla (Fig. 82). In some species, the distal margins of the valves are prolonged into broadly rounded lobes as in *dubius, goodi,* and *digitatus* (Figs. 42-43, 52, 201-202). In others, the distal corner extends into long dactyliform projections of two main types. In *impurus, angularis,* and possibly also *crassatus,* the projections are broad, moderately sclerotized, subequal, and bowed toward each other, the tips touching or nearly so. The stiff, rigid projections resemble opposable digits (Figs. 14, 16, 27-30, 130-132). Valves exhibiting these projections usually lie transversely in the aperture, with the projections from each valve either overlapping or lying next to each other in the midline (Figs. 14, 27, 130). In *compressus,* where the valves lie obliquely in the aperture, the corners extend into unequal, closely appressed projections. That of the inner or medial valve is shorter, subtriangular, and hidden under the very long, rigid, dactyliform extension of the outer valve, which protrudes well beyond the aperture and overhangs the succeeding segment (Figs. 35-37). A similar condition occurs in some populations of *dactylocyphus,* where each valve extends into a long, flexible, dactyliform projection, widely separated from the other, which projects caudad for two more segments (Figs. 187-189). Not all populations of *dactylocyphus* show this extreme development; forms in Victoria County, Texas, possess variable projections ranging from short papillae to longer, digitiform lobes. Regardless of length, the projections of *dactylocyphus* are flexible and widely separated, as opposed to the stiff, rigid ones of *angularis* and *compressus.*

2. *Receptacle.* — Named the "neckpiece" by Causey (1952a) in descriptions of *compressus* and *sanbernardiensis,* the receptacle is located on the closed side of the valves, which is usually lateral. It is also somewhat lower than, or proximal to, the valves and thus does not extend as far ventrad. The receptacle is glabrous, and in many species the corners of its sides curve partly around the operculum, thus partly obscuring it in profile (Figs. 15, 28, 95). In *pulaski* the sides are expanded but are not curved (Fig. 140). Since in other species the sides are neither expanded nor curved, I judge their condition to have taxonomic utility and include it in the diagnoses. In the *melacis* lineage, the receptacle is typically narrow

and compressed into the valves, so as to be barely visible in profile. In *dubius* and *goodi* the receptacle is absent.

Sexual Selection

I have not observed any eurymerodesmids copulating and have no direct knowledge of associated behaviors. Neither are there any published statements, so this section is purely conjectural. However, several aspects of the male and female genitalia differ significantly from those in other chelodesmoids, particularly the Xystodesmidae, and I think bear on this topic. Genetic variation is expressed in most male eurymerodesmids through aspects of the aperture rather than through details of the gonopods as in xystodesmids. Except for *varius,* the gonopods within a species are relatively constant in the Eurymerodesmidae, and *amplus, angularis, birdi, dactylocyphus,* and *digitatus* exhibit a spectrum of aperture variants while maintaining reasonably uniform copulatory appendages. Likewise, females of *impurus, angularis, compressus, crassatus, goodi, dubius, amplus, dactylocyphus,* and *digitatus* possess cyphopods in which the distal margins or corners of the valves are markedly extended, protruding through the cyphopodal aperture *in situ.* Even on species like *varius,* the margins are elevated into a variable rim. Such conditions do not occur in the Xystodesmidae, whose valves are blunt to rounded but never extended. The papillate corner of the rim in some forms of *amplus* and the long dactyliform projections of *compressus* and *dactylocyphus* have the appearance of sensory structures or "feelers," particularly those of *dactylocyphus,* which are flexible. Aside from these structural features, the entire cyphopods of many preserved eurymerodesmid females were extruded through the apertures, with the valves, receptacle, and operculum, lying outside the segment, not just the valvular projections if present. I have rarely observed this condition in xystodesmids.

With these observations of preserved specimens, I turn to the concept of sexual selection by females, advanced by Eberhard (1985) to explain why the male genitalia have species-specific forms in many animals and hence are the source of most taxonomic characters. This hypothesis holds that females discriminate among males of their own species by the structure of the latter's genitalia and that males with favored morphologies produce more offspring, thus promoting rapid, divergent evolution of the male copulatory structures. In some spiders and other organisms the male organ is first inserted into the female before being loaded with sperm; it is then withdrawn, charged with sperm, and reinserted. This process suggests courtship via the male intromittant organ and a "testing" of its configuration by the female. The above observations of eurymerodesmids suggest a different procedure, whereby the female feels or tests the configuration of the male aperture with the cyphopod valves or the valvular projections prior to mating, since individual variation in males is expressed through the aperture. Perhaps the dactyliform appendages actually are "feelers," to test the aperture configuration in advance of mating, and the various distal modifications of the valves represent the variety of female structures that have evolved to accomplish this function.

This hypothesis can be tested in two ways. First, it implies an abundance of sensory cells and neurons in the valvular projections, which can be searched for histologically or through transmission electron microscopy. Secondly, it should be possible to visually observe some sort of pre-mating testing of the male aperture by conspecific females, particularly those of *dactylocyphus* and *compressus,* which have the longest valvular projections. Such observations should be made on captive eurymerodesmids in the laboratory, where they can be watched continuously over time. Observations in the field are more of a chance proposition dependent upon encountering a mating pair at this exact moment, and the mere act of discovery would probably interrupt mating behavior. To date no one has attempted to keep eurymerodesmids alive in a laboratory and rear them, and indeed this has been attempted on very few larger millipeds. Consequently, maintaining live colonies of eurymerodesmids and studying reproductive behavior seem fruitful subjects for future research.

Family Eurymerodesmidae Causey

Eurymerodesmidae Causey, 1951:69; 1952b:1; 1954:67. Chamberlin, 1952:573. Chamberlin and Hoffman, 1958:78. Loomis, 1959:161. Stewart, 1969:384. Reddell, 1970:399. Hoffman, 1979:159.

Type Genus. — Eurymerodesmus Brolemann, 1900.

Diagnosis. — Relatively stiff, inflexible, small to moderate-size Chelodesmidea with the following characteristics: mandibular stipes with basal ridge extending into variable projection on distal corner, usually larger in males; sterna unspined, caudal margins usually straight to slightly curved, with or without variably hirsute elevated areas, lobes, or

knob-like projections adjacent to leg coxae, narrowly or widely segregated in midline, sometimes coalesced into single large structure, projections more pronounced in males, becoming progressively smaller and less hirsute caudally; legs of normal appearance and proportions for suborder, tarsal claws uncinate to slightly bisinuate, with globose basal mass, prefemora without spines and tubercles, with broadly rounded lobes on outer surfaces of pregonopodal legs and varying numbers of postgonopodal legs in males, 2nd coxae of males with variable ventrodistal lobes on anterior and/or caudal margins; gonopodal aperture variably hirsute, configuration highly variable, often elaborately ornamented, anterior margin usually with variable midline indentation, sides elevated to varying degrees, simple or divided to midlength into inner and outer margins, these continuing into inner and outer caudal margins and forming setose pouch or cavity at caudolateral corners, caudal margin with or without variably subtriangular to clavate, densely hirsute lobes at varying distances from caudolateral corners, lobes sometimes enormous and extending well below levels of adjacent coxae; gonopods structurally simple, oriented laterally in aperture with cannula located ventrad or ventrolaterad, connected by membrane only, no sternal remnant; coxae relatively large, without apophyses, with single macroseta located dorsad to cannula; telopodite without prefemoral process, a simple structure directed caudad to caudoventrad from aperture, usually curving near midlength to distal extremity of prefemur; latter varying from 1/3 to 7/8 of telopodite length, comprising entire structure in a few species, with long, dense, matted filiform hairs basally, usually with two to three rows of such hairs along inner margin, and variable distomedial tuft; acropodite not divided, usually varying from about 1/8 to 1/2 of total telopodite length, a very short projection or boss in a few species, usually located apically and poorly demarcated from prefemur, arising from inner prefemoral margin in some forms and subterminally in others; prostatic groove arising in basal pit in prefemur, opening terminally on acropodite; cyphopod valves usually relatively large and moderately hirsute, often with modifications on distal corners ranging from slight ridge to variable dactyliform projections protruding through aperture.

Distribution. — The central, southcentral, and southeastern United States, ranging from northeastern Nebraska, the Missouri River in Missouri, central Illinois, the Fall Zone region of the southeast, and southeastern North Carolina south to northern Florida and the Rio Grande, and westward to the central Great Plains of Kansas and Oklahoma and the Edwards Plateau of Texas (Fig. 1).

Component. — *Eurymerodesmus* Brolemann.

Genus **Eurymerodesmus** Brolemann

Eurymerodesmus Brolemann, 1900:101; 1915:554. Chamberlin, 1920:97-98. Attems, 1938:185. Causey, 1950a:267; 1952a:169; 1952b:1; 1954;67; 1963:77. Chamberlin and Hoffman, 1958:78. Jeekel, 1971:262. Loomis, 1976:287. Hoffman, 1979:159.

Kewanius Chamberlin, 1938:208. Chamberlin and Hoffman, 1958:82. Jeekel, 1971:268.

Paresmus Chamberlin, 1942b:7. Causey, 1950a:271; 1952a:174; 1952b:4. Chamberlin and Hoffman, 1958:82. Jeekel, 1971:278. Hoffman, 1979:159. **NEW SYNONYMY.**

Type species. — Of *Eurymerodesmus, Polydesmus hispidipes* Wood, by monotypy; of *Kewanius, Eurymerodesmus simplex* Chamberlin, by original designation; of *Paresmus, P. paroicus* Chamberlin, by original designation.

Diagnosis. — With the characters of the family.

Color in Life. — Variable; most forms apparently with pink, orange, or red peritremata, color extending slightly onto flattened paranotal surfaces; metaterga varying from speckled black to dark olive-green with concolorous pink, orange, or red stripes along caudal margins connecting peritrematal markings, stripes varying in width, intensity of pigmentation, and partly or completely interrupted to varying degrees by base color; collum with concolorous pink, orange, or red stripes along anterior and posterior margins.

Description. — A genus of small to large eurymerodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size of mature adults varying from large, robust forms of about 6.6 mm wide and 39.5 mm long to minute ones of about 1.6 mm in width and 14.0 mm in length; W/L ratio similarly varying from about 11.3-19.7%. Body essentially parallel sided in midbody region, tapering at both ends, more so caudally.

Head of normal appearance, usually smooth and polished, occasionally partly granular. Epicranial suture distinct, terminating in interantennal region, apically bifid. Interantennal isthmus of varying width. Genae not margined laterally, with or without shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins, width variable. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with four short, conical sensory cones on ultimate article, no other sensory structures apparent. Facial setae reduced; epicranial absent, clypeal and labral present, with or without interantennal, subantennal, frontal, and/or genal series. Mandibular stipes with basal ridge extending into variable projection ranging from minute, rounded, nubbinlike vestige to long, heavily sclerotized structure overhanging gnathochilarium, straight or slightly bowed inward.

Terga smooth and polished, occasionally finely granular, with only trace of wrinkling. Collum considerably longer than remaining tergites, width variable, ends subequal to or extending slightly below those of following tergite. Paranota distinct but relatively narrow; varying from flattened, subparallel to substrate, and thus interrupting slope of dorsum, to variably depressed and relatively continuous with latter; anterior corners broadly rounded on all segments, anterior surfaces excavated to varying degrees, more so in anterior half of body; posterior margins angling anteriad through about segments 5-6, becoming straight in midbody region and angling caudad on posteriormost segments; posterior corners rounded on anteriormost segments, blunt in midbody region, becoming progressively prolonged and acute caudally. Peritremata relatively narrow but thick and conspicuous, strongly set off from paranotal surface, broader caudal to midlength; ozopores located caudal to midlength, opening laterad. Epiproct moderately long and subtriangular, apically narrow and blunt.

Sides of metazonites granular or smooth and polished, with occasional shallow, curved impressions and short, acute projections on first few segments near coxae. Strictures sharp, distinct except on gonopodal segment. Stigmata small, usually rounded. Pregonopodal sterna variously modified; those of segments 2-4 normal; 5th and 6th sterna with variably elevated, flattened areas to narrower paramedian knobs, segregated to varying degrees, elevations and knobs usually higher and more pronounced on 6th sternum, all projections variably hirsute. Postgonopodal sterna with depressions or variably hirsute elevations or projections between 9th legs, segregated to varying degrees or coalesced in midline, usually shorter than widths of adjacent coxae, occasionally subequal to or longer than latter, remaining sterna usually flat, with variably short hirsute projections, or with variable hair patches subtending coxae, becoming progressively less dense caudally, occasionally gently rounded, becoming more plate-like posteriorly, with variable transverse impressions between leg coxae, caudal margin straight in midbody region. Gonapophyses short, truncate, cylindrical, located proximad on 2nd coxae. Legs subequal, of normal length and appearance, 2nd coxae with variable distal projections on anterior and/or caudal surfaces; prefemora without ventrodistal spines, pregonopodal prefemora with variably broad, rounded lobes on outer surfaces, continuing onto postgonopodal legs in most species and terminating around midbody region or on caudal legs, 7th and 9th prefemora occasionally with accessory hooks on anterior surfaces; other podomeres of normal size and appearance on all legs; tarsal claws hooked or slightly bisinute, with slight to distinct basal globose enlargement. Hypoproct broadly rounded, extending slightly mediad; paraprocts with margins narrowly rounded.

Gonopodal aperture extremely variable, often elaborately ornamented, compressing prozonum into variably narrow, inconspicuous band, opening broadly ovoid to elliptical, entire apparatus, including additional space of marginal enlargements, extending laterad to varying distances over pleural regions, configuration varying from essentially a simple oval or rectangle to elaborately trapezoidal; anterior margin usually flush with metazonal surface, almost always with variably broad subtriangular indentation in midline; anterolateral corner rounded, usually flush with metazonum; sides highly variable, usually flush with metazonal surface at anterolateral corner, occasionally flush throughout without modifications or elevations, usually with rim elevated beginning at various distances from anterolateral corner, upright or leaning mediad to varying degrees and obscuring part of opening, raised part either of continuous height throughout or rising slowly or steeply to peak at varying distances caudal to midlength, thereafter either dropping steeply or slowly to metazonal surface, lower elevation on sides, or curving around caudolateral corner for varying distances onto caudal margin, or with densely hirsute, variably broad, and in some forms enormous triangular or clavate lobes arising caudally on sides, at caudolateral corner, or on caudal margin, or divided near midlength with caudal parts of sides and most of caudal margin consisting of two margins, inner lateral margin either extending inward into opening then curving downward, or extending downward and curving and blending into inner caudal margin, thus essentially continuing curvature of anterolateral margin, outer lateral margin angling or flaring caudolaterad to varying degrees at varying distances from division point, either leaning over and obscuring opening or flaring outward immediately, angle of flare varying from imperceptibly slight to around 45°, extending laterad, and in some cases caudad, well beyond levels of stigmata; inner and outer margins forming variable cavities or pouches at caudolateral corners, either partly or completely obscured by angle of flare and/or lean of outer lateral margin or open with strongly flared outer lateral margin; caudolateral corner variably rounded, blunt or angled, rim flush or elevated to varying degrees and with or without lobes, usually continuous with lateral margin, forms with two margins also with inner and outer caudolateral corners, former flush with metazonal surface and usually smoothly curved, visible or obscured to varying degrees by outer lateral margin, outer caudolateral corner rounded, blunt or angled, elevated to varying degrees above metazonal surface, usually continuous with outer lateral margin; caudal margin linear or curving smoothly on anterior side of 9th legs, frequently extending caudad medially and terminating between 9th legs, occasionally merging with sternal projections between latter, margin usually elevated laterally, continuous with sides, elevations tapering or dropping abruptly to metazonal surface at varying distances from caudolateral corner, increasing in some forms into variably short to enormous triangular or clavate lobes; forms with pouches and inner and outer lateral margins also with inner and outer caudal margins, former smoothly continuous with inner lateral margin, flush with metazonal surface, either completely inside and essentially parallel to outer caudal margin or merging with latter near midline, outer caudal margin usually elevated laterad, continuous with flare or outer lateral margin at caudolateral corner, tapering to metazonal surface and continuing along anterior side of 9th legs; aperture margins variably hirsute, with or without long filiform hairs arising from rim and overhanging opening, shorter and stouter hairs on outer surfaces of lateral and/or outer lateral margins, and variably dense tufts from pouches; anterior margin often with 3-6 long hairs along indentation and scattered hairs elsewhere; lateral margin with sporadic hairs from rims on anterior halves, hairs on outer surface usually restricted to caudal halves of sides; marginal lobes densely pilose with very short hairs arising from base to tip or with hairs becoming progressively denser and longer distad; caudal margin lightly hirsute or glabrous, usually with at most only a single row of sporadic hairs. Gonopods *in situ* with telopodites curving variably caudoventrad from coxa, touching, overlapping, or narrowly or widely segregated in midline, extending over caudal margin(s) to varying degrees with apices directed sublaterad or subdorsad. Coxae relatively large, usually attaching under lateral margins of aperture and directed caudomediad, cannulas located ventrolaterad to ventrad, curving ventrad and inserting into pit of prostatic groove in base of prefemur, without apophyses but often extending slightly ventrad behind base of prefemur, connected by membrane only, without sternal remnant. Telopodite of variable length, terminating before, at, or beyond distal extremities of

hairs. Prefemur of variable length and width, usually comprising from 1/3 to 7/8 of telopodite length, in some forms constituting all of latter, arising ventrally on coxa and extending mediad basally, closely appressed to and slightly submerged in coxa, curving or bending ventrad at or just before medial margin of latter and continuing linearly or in slightly bowed or curved configurations, with or without slight to moderate distal lobe or shoulder on outer or inner surfaces; usually with dense mass of filamentous hairs, usually with two to three rows of long, variably spaced filamentous hairs along inner and lateral surfaces of stem demarcating prostatic groove, some forms with nearly glabrous stems or with only a few scattered hairs, usually with distomedial tuft of from 4 to 15-18 hairs. Acropodite usually subtriangular to long, slender, and subacicular, arising apically or subterminally on prefemur, when apical smoothly continuous with and poorly demarcated from prefemur, or discontinuous and sharply demarcated, restricted to inside or outside of prefemur, length varying from about 1/8 to 2/3 of telopodite length, smoothly curved to sublinear, sides tapering smoothly and continuously to variably acuminate to blunt tip; acropodite occasionally very short, nubbinlike to a rudimentary boss, arising subterminally on inner surface of prefemur, shielded by distal lobe of latter and/or submerged in cavity along inner margin. Prostatic groove arising in basal pit in prefemur, running along inner surface of latter to terminal opening on acropodite.

Females usually slightly larger than conspecific males. Agreeing essentially with latter in somatic features with following exceptions: Process of mandibular stipes usually much shorter, a small nubbinlike vestige to slightly larger rounded lobe. Paranota narrower and more strongly depressed, continuing slope of dorsum, creating appearance of more highly arched or vaulted body. Sterna usually flattened and nearly glabrous, transverse grooves less pronounced and becoming even fainter caudally, without lobes, with sparse hair patches subtending coxae, hairs becoming even sparser caudally. 2nd coxa without lobes or projections. Prefemora without lobes on outer surfaces.

Cyphopodal aperture variably rectangular, ovoid, or elliptical, sides flush with metazonal surface or moderately to strongly elevated, occasionally flared. Cyphopods *in situ* either transverse, oblique, or perpendicular to body axis, valves usually anterior/posterior to each other with edges or valvular projections visible in, or protruding through opening, valves occasionally dorsoventrad to each other in transverse arrangement with edges invisible, or arranged along body axis with valves laterad/mediad to each other and edges visible in opening; corner (tip) of receptacle often visible *in situ*. Valves varying in size, subequal to unequal with either valve larger, distal surfaces variably hirsute, hairs increasing proximad, with or without variable lobes or linear, angular, papillate, or dactyliform projections usually arising from distal margins, usually directed ventrad. Receptacle generally subtriangular, located laterad, caudad, or dorsad to valves, occasionally submerged in latter to varying degrees, usually smaller than valves, glabrous, sides either curving distad and partly enclosing or obscuring operculum or not. Operculum varying in size, small to moderately large, triangular in profile, oblong in frontal view, with long, curved hairs arising from outer surface.

Synonymy. — Causey (1963) placed *Kewanius* in synonymy under *Eurymerodesmus* based on an examination of the holotype of *E. simplex,* the type species. However, she gave no reasons or illustrations, merely stating that she found no characters justifying a new taxon. Hoffman (1979) retained this synonymy. *Paresmus* was proposed largely because of the stouter gonopod of *paroicus,* the type species (Chamberlin 1942b, Causey 1950a), and Chamberlin also indicated that the structure was distally notched instead of acuminate. However, the most significant feature of *paroicus* is the subterminal acropodite (Figs. 124-125), also displayed by *pulaski* (Figs. 136, 138), described in *Paresmus* by Causey (1950a). In *polkensis,* assigned to *Paresmus* in the original description (Causey 1952b), the acropodite arises terminally but only from the inner prefemoral margin. The outer prefemoral surface forms a shoulder above the acropodite (Figs. 111-113, 115). The two other species currently in *Paresmus, impurus* and *columbus,* have broadly terminal acropodites, moderately wide telopodites, and are readily accommodated by *Eurymerodesmus;* the latter is placed in synonymy under *dubius,* although its type is lost and this action should be corroborated by topotypes. Thus *paroicus, pulaski,* and *polkensis* differ primarily in the size of the apical lobe on the outer surface of the prefemur. In the former two species it is very large, overhanging and extending well beyond the level of the acropodite, which therefore arises subterminally. In the latter species, the lobe is not expanded, does not overhang the acropodite, and therefore constitutes a shoulder. Neither Chamberlin (1920) nor Causey (1963) illustrated *simplex,* but as shown in figures 104-105, it displays the configuration of *polkensis* with a longer acropodite and a broader, clavate, and more rounded shoulder. Consequently, the form represented by *paroicus* and referrable to *Paresmus,* with a subterminal acropodite and an expanded distal prefemoral lobe, can be derived from that represented by *simplex* and referrable to *Kewanius* through enlargement of the prefemoral shoulder such that it extends beyond the acropodite and causes the latter to arise subterminally. Therefore, *Paresmus* should at least be considered a synonym of *Kewanius,* which has four years of priority for forms with distal prefemoral lobes or shoulders. As shown in figure 65, populations of *varius christianus* in Louisiana also display an apical lobe on the outer surface of the prefemur. This feature is less distinct in intergrade forms in Mississippi (Fig. 63), and it disappears entirely in the nominate race on the Atlantic Coast (Figs. 57-58), which is clearly referrable to *Eurymerodesmus.* Thus, a transformation series exists from the subterminal acropodites of *paroicus* and *pulaski,* to the terminal ones on the inner prefemoral margins of *polkensis* and *simplex,* to the lobed forms of *varius christianus* in Louisiana, to the eastern populations of *varius varius* with broadly

terminal, poorly demarcated acropodites, subequal in width to the distal extremity of the prefemur. Consequently, it follows that *Paresmus* as well as *Kewanius* must fall as synonyms of *Eurymerodesmus.*

Distribution. — Same as that of the family.

Species. — 25, arranged into four lineages. Two species are subdivided into a total of five geographic races. Future studies based on significantly more material may show that *angularis* and *amplus* should be divided into additional localized forms, recognizable at the specific level, and undoubtedly many more localized forms remain to be discovered in the *Kewanius* and *melacis* lineages. As stated in the introduction, however, these localized forms may not possess the full properties of species and may actually constitute semispecies, in contrast to *birdi* and *mundus,* which are unquestionably reproductively isolated. Resolution of this theoretical matter is beyond the scope of the present revision, where for consistency with recent studies, particularly that on *Sigmoria* (Shelley and Whitehead 1986), I recognize all apparently distinct, localized forms as well as *birdi* and *mundus* at the specific level. Depending upon how this question is resolved, *Eurymerodesmus* will either have many more or less than 25 species, the former if the localized forms are evaluated as reproductively isolated, and the latter if they are found to be less than full species. Conceivably, *Eurymerodesmus* may have as few as five species: *hispidipes, birdi,* and *mundus,* plus the *melacis* and *Kewanius* lineages collectively.

Remarks. — Although this study is based on examinations of over 2,000 preserved specimens, *Eurymerodesmus* is far from thoroughly sampled. This is particularly apparent in southern Arkansas and northern Louisiana, the area with the most diverse fauna. Fourteen species (*mundus, birdi, angularis, amplus, dubius, paroicus, pulaski, crassatus, compressus, polkensis, goodi, hispidipes, simplex,* and *varius*), 56% of the total known fauna, occur there, with *birdi* represented by both subspecies and *varius* represented by *v. christianus* and *v. louisianae* (Fig. 211). Consequently, this region should be meticulously sampled to determine actual distributions. My brief forays into southern and central Illinois, the New Orleans region of Louisiana, and Texas south of Houston and Austin were not very productive and convinced me that adequate collecting in the areas of high diversity would take years and could only be accomplished by someone based there. The forested part of east Texas, generally north of Houston and east of Dallas, is another region needing attention.

Without more material and refined knowledge of distributions, particularly in these states, decisions on affinities and compositions of lineages and species groups are tentative. Anatomical patterns can be detected in both the gonopods and the aperture, but without better knowledge of their distributions, decisions on relationships are imperfect. Another difficulty is matching sexes, since some samples may contain males of one species and females of another, for example the type series of *angularis* and *crassatus,* and the neotype sample of *pulaski,* which also contained specimens of *serratus.* Careful field work is needed to check for and record subtle differences in behavior, color patterns, and microhabitat, which may indicate different species. Some questionable samples may contain forms found close together but in different microhabitats, which cannot be determined from faded, blanched specimens and without detailed habitat information on vial labels; others may contain forms from relatively close, but nevertheless distinct sites. Thus, females may not be matched with conspecific males in some species accounts, and the following descriptions and species groupings are only approximations based on the incomplete available material. There is ample room for additional investigation by someone with the time to conduct meticulous field surveys, particularly along range peripheries, and record detailed habitat and color data.

Key to Species of **Eurymerodesmus**
(based primarily on adult males)

Because of great variation in such species as *angularis, amplus, birdi,* and *varius,* and phenotypic similarities between variants of others, for example between *oliphantus* and forms of *amplus,* a key to species of *Eurymerodesmus* is very difficult to devise. Few comments can be made about any one species that do not also apply to another, and the total range of variation in many species is such that little can be said that will not exclude an important variant Added to these standard difficulties with speciose milliped genera are the complexities of the aperture and the inherent difficulties in drawing the structure, verbalizing it, and combining these into meaningful couplets. Consequently, this key has limited utility and is best viewed as an introduction, perhaps more suited to eliminating taxa than to obtaining absolute determinations. Use it to reach one or two final couplets then compare the form in ques-

tion with the appropriate illustrations and descriptive accounts for final determinations. For this purpose, I have incorporated figure references throughout the key and attempted to provide more descriptive detail on variation than usual. The distinctive cyphopods of *dactylocyphus, impurus, angularis, compressus,* and *amplus* are also incorporated into the key, and females of these species may be easier to recognize than males. *Eurymerodesmus varius* appears twice, to cover forms with and without prefemoral lobes, and its three subspecies are keyed in the species account. Subspecies appear herein for *birdi.* Generalized range descriptions are also provided since the aforementioned difficulties indicate the probability of more geographically based determinations for *Eurymerodesmus* than for most revised milliped taxa.

1. Acropodite very long, comprising at least half of telopodite length (Figs. 12-13, 19-20, 22, 24, 26, 40-41) 2
   Acropodite much shorter, comprising much less than half of telopodite (Figs. 7-8, 33-34, 47-48, 57-58, 63, 65, 69-70, 74-75, 104-105, 111-112, 124-125, 128-129, 135-136, 143-145, 152-153, 206-207) 4
2. Sides of aperture entire, elevating slowly to peak at or near caudolateral corner (Fig. 39); corners of cyphopod valves rounded but not extending into segregated projections (Figs. 42-44); Polk and Montgomery cos., AR ..... *goodi* Causey
   Sides of aperture either slightly to moderately elevated and divided caudally into inner and outer margins forming caudolateral pouches (Figs. 18, 21, 23, 25), or undivided but greatly elevated with cupulate flange extending beyond caudolateral corner and forming an apparent but false pouch between inner surface and metazonum (Fig. 11); distal corners of cyphopod valves extending into rigid segregated projections, usually bowed towards each other with apices touching or nearly so, occasionally directed oppositely (Figs. 14, 16, 27-30) 3
3. Sides of aperture slightly to moderately elevated and divided, with caudolateral pouches (Figs. 18, 21, 23 25); projections of cyphopod valves relatively narrow, dactyliform (Figs. 27-30); central MO to northern LA and eastern MS ..... *angularis* Causey
   Sides of aperture strongly elevated but not divided, without true caudolateral pouches (Fig. 11); projections of cyphopod valves relatively broad, not dactyliform (Figs. 14-16); Brazos and Washington cos., TX ..... *impurus* (Wood)
4. Sides of aperture divided caudally into inner and outer margins, with variably open to closed caudolateral pouches (Figs. 56, 59, 76-78, 84, 91, 97, 103, 123) 5
   Sides of aperture entire, without pouches (Figs. 6, 46, 109, 117, 134, 142, 149, 157, 162, 169, 178, 184, 191) 18
5. Acropodite essentially smoothly continuous with, and poorly demarcated from prefemur; latter with at most only very slight distal swelling on outer margin (Figs. 33-34, 47-48, 57-58, 63, 74-75, 85-86) 6
   Acropodite not smoothly continuous with prefemur, either subterminal (Figs. 124-125, 128-129, 135-136, 143-145); terminal and discontinuous, arising from inner prefemoral margin (Figs. 104-105, 111-113, 118-119); or terminal and continuous but sharply demarcated from prefemur, latter with strong distal lobe on outer margin (Figs. 64, 71) 11
6. Prefemur sparsely or lightly hirsute, with light distomedial tuft and at most scattered, sporadic hairs along stem, hairs arranged irregularly, with variable and sometimes sizeable intervening gaps (Figs. 57-58, 63); southern AR and western LA to FL and NC ..... *varius* (McNeill)
   Prefemur moderately to densely hirsute, with variable distomedial tuft and relatively continuous hairs along stem, hairs arranged regularly or irregularly, but without sizeable gaps (Figs. 33-34, 74-75, 85-86, 92-93, 98-99) 7
7. Acropodite moderately long, longer than 1/4 of telopodite length, broad for most of length, compressed laterally; prefemur without trace of distal swelling (Figs. 33-34); distal corners of cyphopod valves extended into rigid, unequal, and closely appressed projections, that of outer (lateral) valve very long and narrow, dactyliform, protruding well beyond aperture and overhanging succeeding segment (Figs. 35-37); Union Co., AR ..... *compressus* Causey
   Acropodite short, no more than 1/4 of telopodite length, relatively narrow with sides usually tapering rapidly, not compressed; prefemur usually with slight but detectable distal swelling (Figs. 74-75, 85-86, 92-93, 98-99); corners of cyphopod valves without dactyliform projections, either not or indistinctly extended into angular ridge, with or without terminal papilla 8
8. Acropodite distinctly uncinate, curving downward or dorsolaterad throughout length (Figs. 85-86); caudolateral pouch partly closed, covered by lean of outer lateral margin (Fig. 84); Benton, Washington, and Newton cos., AR ..... *newtonus* Chamberlin
   Acropodite either straight or curving distal to midlength (Figs. 74-75, 92-93, 98-99); caudolateral pouch closed to open (Figs. 73, 76-78, 91, 97) 9
9. Outer lateral margin rising continuously into broad, elevated lobe at caudolateral corner, not flaring laterad; inner lateral margin forming floor of pouch, cavity mostly on cupped inner surface of elevation (Fig. 97); Cole and Morgan cos., MO ..... *elevatus,* new species
   Outer lateral margin variably rising but not forming elevated lobe, flaring variably laterad; inner lateral margin forming inner edge of pouch, cavity between outer and inner margins (Figs. 73, 76-78, 91) 10
10. Caudolateral pouch broadly open, outer lateral margin flaring strongly caudolaterad, revealing, entire inner margin in ventral view, outer surface of outer lateral margin only slightly visible (Fig. 91); corners of cyphopod valves not produced (Figs. 94-95); southern IL to north-central AR ..... *oliphantus* Chamberlin
    Caudolateral pouch variable, partly open to completely closed, inner margin usually partly obscured by lean of outer lateral margin, latter with considerable part of outer surface visible in ventral view (Figs. 73, 76-78); corners of cyphopod valves either imperceptibly extended or produced into angular ridge of variable length, with or without terminal papilla (Figs. 80-82); west of Mississippi River in LA to Wood and Grimes cos., TX, with allopatric population in Mason Co, TX. ..... *amplus* Causey

11. Acropodite arising subterminally from prefemur; latter variable distad but forming terminal part of telopodite (Figs. 124-125, 128-129, 135-136, 138, 143-145) 12
Acropodite arising terminally, either exclusively from inner prefemoral margin (Figs. 104-105, 111-113, 115, 118-119) or sharply demarcated by strong distal lobe on outer prefemoral surface (Figs. 65, 71) 15
12. Terminal part of prefemur broadly expanded, margin irregularly serrate to jagged (Figs. 143-145); Pulaski Co., AR, and Alachua Co., FL ..... *serratus,* new species
Terminal part of prefemur variably elongate but not expanded or wide, tapering to blunt or subacuminate tip, margins smooth (Figs. 124-125, 128-129, 135-136, 138) 13
13. Acropodite a thickened inconspicuous boss hidden in excavation or concavity on inner surface of prefemur, terminal part of latter either sublinear or apically uncinate (Figs. 135-136, 138); Pulaski Co., AR ..... *pulaski* (Causey)
Acropodite varying from a minute nubbinlike projection to a short spur extending clearly from inner surface of prefemur; latter not excavated (Figs. 124-125, 128-129) 14
14. Acropodite nubbinlike, indistinct; prefemur with inner margin irregular, terminal part broadly rounded (Figs. 128-129) ..... *crassatus,* new species
Acropodite a short, distinct spur; prefemur with inner margin smooth, terminal part tapering to subacuminate tip (Figs. 124-125) ..... *paroicus* (Chamberlin)
15. Acropodite broadly terminal but strongly demarcated from prefemur; latter with outer margin expanding distad into rounded lobe (Figs. 65, 71), southern AR and western LA to FL and NC ..... *varius* (McNeill)
Acropodite narrowly terminal, arising exclusively from inner margin of prefemur (Figs. 104-105, 111-113, 115, 118-119) 16
16. Prefemur distally clavate, sides expanding throughout length to distinct shoulder on outer margin (Figs. 104-105); Evangeline Par.,LA ..... *simplex* Chamberlin
Prefemur with sides relatively parallel throughout (Figs. 111-113, 118-119) 17
17. Terminal margin of prefemur with closely packed, thick hairs forming semicircular corona, lying parallel to and partly obscuring acropodite, telopodite thus appearing to terminate in calyx; aperture without anterior indentation (Figs. 117-119); Franklin Co., MS ..... *caesariatus,* new species
Terminal margin of prefemur without hairs, acropodite clearly visible; aperture with anterior indentation (Figs. 109-115); Polk Co., AR ..... *polkensis* (Causey)
18. Sides of aperture and/or caudolateral corner distinctly elevated above metazonal surface, with or without lobes at corner or on caudal margin (Figs. 6, 149, 154, 157, 169) 19
Sides of aperture and caudolateral corner essentially flush with metazonal surface (Figs. 162, 165, 178, 184, 191) 21
19. Aperture without distinct lobes, marginal elevation of relatively uniform height, extending around caudolateral corner onto caudal margin (Fig. 6); Coles Co., IL, and Ashley Co., AR ..... *hispidipes* (Wood)
Aperture with densely hirsute, variable lobes on caudal margin or at caudolateral corner (Figs. 149, 154, 157, 169) 20
20. Aperture lobes clavate, very large, clearly located on caudal margin, distinctly removed from caudolateral corner (Figs. 169-171); northeastern NE to western AR and Johnson CO., TX ..... *mundus* Chamberlin
Aperture lobes short to long, variably triangular, never clavate, variably higher than marginal elevation, located at caudolateral corner or on caudal margin at varying distances from latter (Figs. 149-151, 154-158); eastern KS and central MO to San Patricio Co., TX, Warren Co., MS, and Jefferson Par., LA ..... *birdi birdi* Chamberlin
21. Acropodite narrowly terminal, arising from outer surface of prefemur; latter distally clavate with shoulder on inner margin Figs. 206-207); Austin Co., TX ..... *clavata,* new species
Acropodite broadly terminal, smoothly continuous with, and poorly demarcated from prefemur; latter of more or less continuous width throughout, with or without slight distal swellings but without distinct shoulder, not clavate (Figs. 163-164, 179-180, 185-186, 192-193, 199-200) 22
22. Telopodites relatively long, extending distinctly beyond caudal margin of aperture and overhanging 9th coxae or sternum between same (Figs. 162, 165); Rankin Co., MS, to Orleans Par., LA ..... *birdi planus* Causey
Telopodites relatively short, either wholly enclosed by aperture or barely overhanging caudal margin (Fig. 178, 184,191, 198) 23
23. Aperture very broad, covering essentially entire breadth of segment in ventral view and wholly encompassing telopodites, caudolateral corners elevated into variable flange (Fig. 184); distal corners of cyphopod valves extending into variable papillate to dactyliform projections, latter flexible, protruding well beyond aperture and overhanging succeeding segments (Fig. 187); Bosque to Victoria cos., TX ..... *dactylocyphus,* new species
Aperture much smaller, extending to or only slightly beyond levels of stigmata, not nearly covering entire breadth of segment, telopodites either enclosed within aperture or slightly overlapping caudal margin, caudolateral corners at most only slightly elevated, not forming flange (Figs. 178, 191, 198); cyphopod valves variable but without dactyliform projections (Figs. 181-182, 194-195, 202-203) 24
24. Acropodite bending strongly laterad (Figs. 178-180); Taylor to Terrell and Hidalgo cos., TX ..... *melacis* Chamberlin and Mulaik
Acropodite curving gently or strongly dorsad (Figs. 191-193, 198-200) 25
25. Caudal margin of aperture extending caudad in midline (Fig. 191); acropodite strongly curved (Figs. 192-193); Colorado to Brazoria cos., TX ..... *sanbernadiensis* Causey
Caudal margin of aperture linear (Fig. 198); acropodite gently curved, nearly upright (Figs. 199-200); Comanche Co., OK, to Blanco Co., TX ..... *digitatus* Loomis

The **Hispidipes** Lineage

With raised, vertical, laminate lateral margins that curve around the caudolateral corner for about 1/3 of the length of the caudal margin, *hispidipes* differs from all congeners and merits a separate species group and lineage, which will become the nominate subgenus if these categories are shown by future studies to warrant taxonomic recognition. In other species lacking caudolateral pouches, the aperture elevations are thicker and not laminate. The slightly higher and more densely hirsute terminus of the elevation on the caudal margin faintly suggests a lobe, a possible indication of affinity to the *birdi* lineage, most forms of which possess densely hirsute lobes in this position. The *hispidipes* lineage is composed of one species group and one species.

Eurymerodesmus hispidipes (Wood)
Figs. 2-9, 211

Polydesmus (Polydesmus) hispidipes Wood, 1864:7-8.
Polydesmus (Paradesmus) hispidipes Wood, 1865:220, fig. 48.
Leptodesmus hispidipes: Bollman, 1893:122.
Eurymerodesmus hispidipes: Brolemann, 1915:554. Attems, 1938:185, fig. 203. Chamberlin and Hoffman, 1958:191 (in part).

Type specimens. — Two fragmented male syntypes and segments 4-7 of one female (NMNH) collected by R. Kennicott on an unknown date from an unknown site in Illinois. Wood (1864, 1865) did not mention a holotype nor are any of the fragments so designated, and it is impossible to match pieces to form a complete individual. I therefore regard this material as syntypical. There is a jar labeled "paratype" at the ANSP, also from Illinois by R. Kennicott and therefore probably from the same series, which consists of shards and debris. The number of specimens and sexes are unknown, but I noticed nothing resembling gonopods or an aperture when sifting through it in 1987. The sample is thus useless. Wood (1864, 1865) refers to 18 males in the original descriptions, an unknown number of which is probably among the debris at the ANSP. For practical purposes only the two fragmented males at the NMNH survive.

Diagnosis. — A small to moderate-size species; males characterized by moderate mandibular projections; sides of aperture undivided, without caudolateral pouches, with vertical, laminate elevation curving around caudolateral corner and becoming progressively higher, terminating abruptly about 1/3 of length of caudal margin; telopodite moderately long; acropodite short, about 1/8 of telopodite length, and broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged relatively continuously along inner surface of stem; females unknown.

Color in Life. — Unknown.

Male syntypes. — Bodies highly fragmented, lengths unmeasurable, maximum width 3.3 mm.

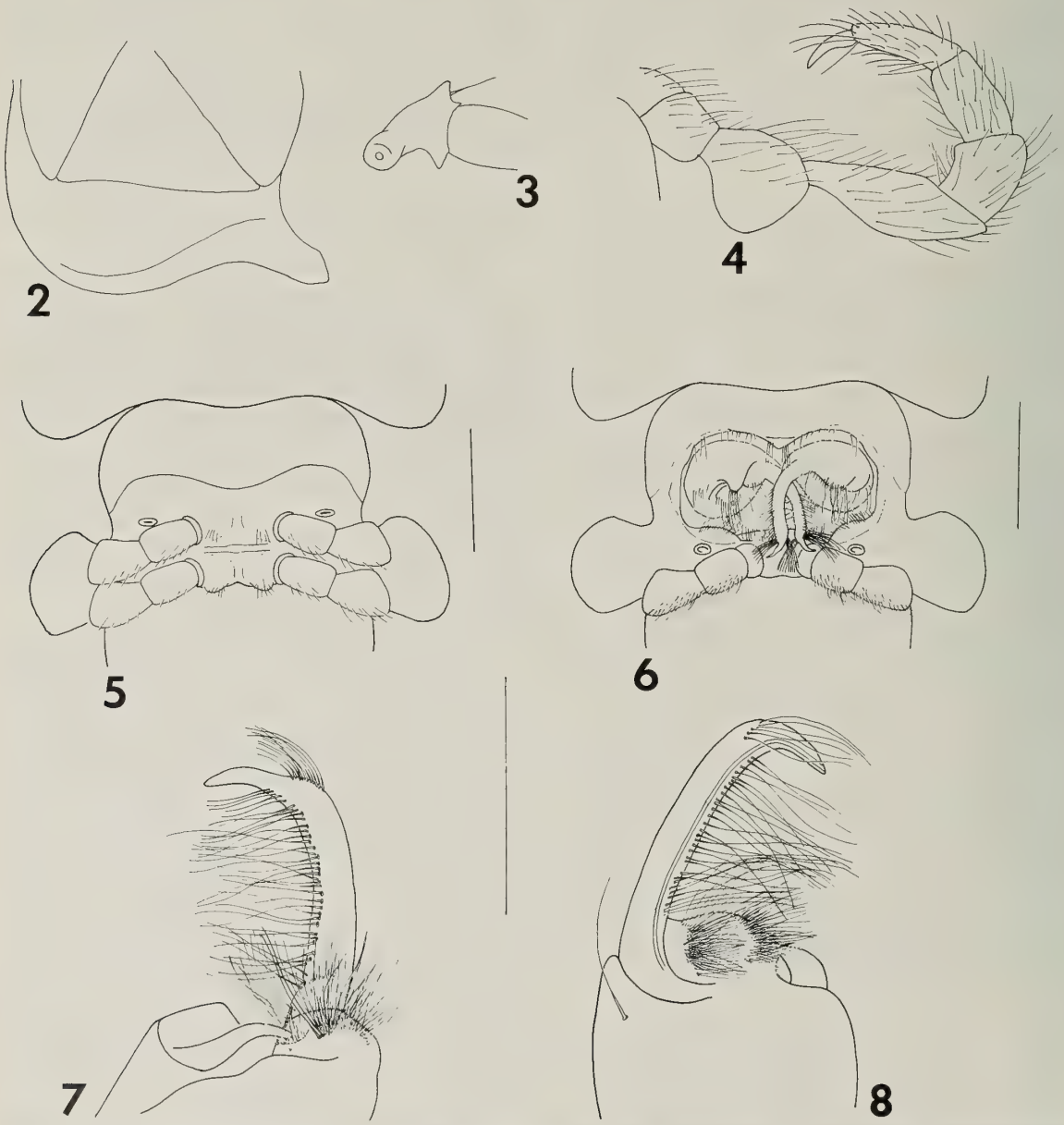
Head capsule smooth, polished or slightly granular, width across genal apices 2.8 mm; interantennal isthmus 0.9 mm, smooth; epicranial suture narrow, linear, terminating in interantennal region, apically bifid. Antennae reaching back to caudal margin of 2nd tergite, moderately hirsute throughout, first antennomere subglobose, 2-6 clavate, 7 short and truncate; relative lengths of antennomeres $2=6>3=4=5>1>7$, with four apical sensory cones, no other sensory structures evident. Genae not margined laterally, with distinct central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Facial setae as follows: epicranial, interantennal, frontal, and genal absent; clypeal about 4-4; labral about 9-9. Mandibular stipes with broad projection, in lateral view overhanging lingua lamella of gnathochilarium, tapering slightly distad to rounded tip on inner corner (Fig. 2).

Terga smooth, polished or slightly granular; paranota with only faint wrinkling anteriorly on inner surface. Collum broad, considerably longer than succeeding tergites, ends extending slightly below those of following tergite, corners narrowly rounded. Paranota distinct but relatively narrow, flattened and subparallel to substrate, interrupting slope of dorsum; anterior corners broadly rounded with inner dorsal surface strongly excavated in anterior half of body, becoming progressively narrower, straighter, and less excavated caudally; posterior margins angling anteriad through segment 5, corners blunt on anterior segments, becoming progressively prolonged and acute posteriorly. Peritremata relatively narrow but thick and conspicuous, strongly set off from paranotal surface, broader caudal to midlength. Ozopores located caudal to midlength, opening laterad. Epiproct moderately long and subtriangular, apically narrow and blunt.

Sides of metazonites granular, with occasional shallow, curved impressions. Strictures narrow but distinct, forming bisinuate curve on ambulatory segments (Fig. 5), displaced anteriad by aperture on segment 7 (Fig. 6). Sternum of segment 5 slightly elevated and hirsute adjacent to leg coxae; that of segment 6 with elevations stronger, broader, and more densely hirsute. Postgonopodal sterna with transverse impressions between leg coxae varying from strong and completely crossing 8th sternum to indistinct on 18th sternum; surface otherwise flat to gently rounded, caudal margin straight in midbody region, becoming progressively more indented medially caudad. Legs without spines, moderately and relatively equally hirsute throughout, prefemora expanding into broadly rounded lobes on outer margins, lobes present on pregonopodal legs, becoming smaller in midbody region and diminishing thereafter; femur generally longer than other podomeres, tarsal claw varying from straight to moderately hooked (Fig. 4). Gonapophysis short, cylindrical, truncate; 2nd coxa with subconical distal lobes on anterior and posterior margins, former slightly larger with one seta (Fig. 3). Hypoproct broadly rounded, extending slightly mediad; paraprocts with margins slightly thickened.

Gonopodal aperture (Fig. 6) broadly ovoid, without caudolateral pouch, indented anteriad at midline, 1.9 mm wide and 1.1 mm long at midpoint, outline of entire apparatus moderately broadly ovoid; anterior margin flush with metazonal surface, narrowing mediad and extending into opening as short,

broadly triangular projection; sides sublinear, not divided, slightly indented and flush with metazonal surface at anterolateral corners, becoming progressively more elevated caudally and continuing without interruption about 1/3 of distance onto caudal margin, essentially linear, leaning slightly over opening, rims smooth; caudolateral corner broadly rounded, nearly a right angle; caudal margin continuing elevation of sides, elevating slightly and becoming more rounded, then terminating abruptly well short of midline at about 1/3 length; margins irregularly hirsute with long hairs arising sporadically from anterior and caudal margins and overhanging opening, former with small tufts on sides of indentation and several other marginal hairs, sides relatively glabrous, caudal margin with moderately dense tufts on elevation, hairs also arising from outer surface caudally and caudolaterally, continuing in linear arrangement along recessed part of margin between lobes. Gonopods *in situ* (Fig. 6) with telopodites directed caudoventrad, curving slightly across midline and crossing opposite member, extending over caudal margin in midline and overhanging sternum between 9th legs. Gonopod structure as follows (Figs. 7-8): Telopodite moderately long, terminating before level of distal extremities of hairs. Prefemur relatively long, about 7/8 of telopodite length, linear, tapering slightly near midlength and curving broadly caudoventrad, with two rows of long, regularly spaced hairs arising from inner margin and distomedial tuft of ten or so



Figs. 2-8. *Eurymerodesmus hispidipes*. 2, right mandibular projection of syntype, lateral view. 3, left 2nd coxa of syntype, ventral view. 4, left 7th leg of male from Coles Co., IL, caudal view. 5, segment 8 of the same, ventral view. 6, aperture and gonopods *in situ* of syntype, ventral view. 7, left gonopod of the same, lateral view. 8, the same, medial view. Scale lines for figs. 5-6 = 1.00 mm. Line for other figs. = 0.60 mm for 2-3, 0.50 mm for 4, and 1.00 mm for 7-8.

hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, arising apically at slight constriction of prefemur, directed dorsad, slightly hooked or bisinuate, tapering rapidly to subacuminate tip.

Female Syntype. — Among the fragments in the NMNH sample are segments 4-7 of a female, which lack structural peculiarities. The sterna resemble caudal postogonopodal sterna of males with incomplete transverse grooves between the leg pairs. Segment 3 is missing, and Wood's descriptions of the cyphopods (1864, 1865) do not reveal significant features. Thus for practical purposes, females of *hispidipes* are unknown.

Variation. — Wood (1864, 1865) noted differences in color among individuals in the type series. He suggested that they might represent a distinct species but did not propose a name because of similarities in the genitalia. Since all traces of color and pattern have vanished after 125 years in preservative, I cannot confirm Wood's observations. However, the gonopods of the two surviving males differ in that the acropodites of one are bisinuate and more strongly demarcated from the prefemur, while those of the other are slightly curved. The aperture configurations are practically identical. The left lateral margin of the Coles County male flares outward slightly caudolaterad, whereas the margin on the right is straight. The acropodites of this specimen are slightly bisinuate and moderately demarcated from the prefemur. The degree of hirsuteness of the aperture is subsimilar to that in the syntypes, and the only facial setae present are the clypeal (about 11-11) and labral (about 14-14) series. The Arkansas male possesses a few scattered hairs on the lateral margins, but otherwise the aperture and gonopods closely resemble those of the Coles County male. Facial setae of the Arkansas male are subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 10-10, and labral about 18-18. The specimen measures 22.0 mm in length, 3.9 mm in width, W/L ratio 17.7%.

Ecology. — The Coles County specimen was taken from a clod of dirt in a ploughed field. Nothing is known about the habitat of either the type series or the Arkansas specimen.

Distribution. — Known definitely only from Coles County, Illinois, and Ashley County, Arkansas (Fig. 9). Wood (1864, 1865) did not specify a site or general area in Illinois, and the record from Dixon Springs, Pope County (Causey 1950a, Chamberlin and Hoffman 1958), incorrectly placed in Lee County by the latter authors, refers to *oliphantus*. Specimens were examined as follows:

ILLINOIS. Unspecified locality and date, 2M, F, R. Kennicott (NMNH) SYNTYPES and unknown number of specimens (ANSP) "PARATYPES." *Coles Co.,* Charleston, Normal School (now Eastern Illinois University), M, 13 May 1918, T. L. H. (EIU, transferred to NCSM).

ARKANSAS. *Ashley Co.,* 6.1 mi. E. Hamburg, M, 23 April 1965, collector unknown (FSCA).

Remarks. — The two known localities are separated by about 470 miles, a great distance casting doubt on the accuracy of the Arkansas record. However, other eurymerodesmids cover large areas and have samples from disparate localities known to be correct, most notably *serratus* from Pulaski County, AR, and Alachua County, FL. I therefore consider the Arkansas record to be correct and show it in the distribution map (Fig. 9).

On May 20, 1989, 81 years and one week after collection of the Coles County male, I revisited this area of eastern Illinois to attempt to secure more material, particularly of females, whose genitalia are unknown. I spent two days working in wooded areas along the Fox River and tributaries, and turning logs and rocks in clearings, all to no avail. I therefore believe that this male represents a thoroughly fortuitous discovery and that future collections are as likely to occur through chance accidents as through planned, systematic field work.

For years *hispidipes* was considered the only or most abundant species of the genus and family, and the name was routinely applied to forms in other parts of the generic range as recently as 1969, after many other nominal species had been diagnosed. I have examined the specimens on which some of these records are based and review them in Table 3 below. Others are lost but can be assigned reasonably accurately to one or two species from knowledge of distributions. All references to *hispidipes* are cited in the synonymies of the appropriate species. Since they actually refer to Wood's original citations, only Bollman (1893), Brolemann (1915), Attems (1938), and Chamberlin and Hoffman (1958) cite *hispidipes* correctly at least in part.

The **Kewanius** Lineage

I combine in one lineage all species in which the sides of the aperture are divided caudally into inner and outer margins with pouches at the caudolateral corners, or which appear related to such species through shared traits of the gonopods or aperture. The assemblage is heterogeneous, but all com-

Table 3. Previous literature citations of *hispidipes*.

Author	Date	Locality	Species
Wood	1864, 1865	Original descriptions, unspecified site in IL	*hispidipes*
Bollman	1888a	Unspecified sites in AR	*pulaski, serratus,* and perhaps others
Bollman	1893	Refers to original description	*hispidipes*
Brolemann	1895	Unspecified site in LA	*amplus*
Brolemann	1900	None	probably *amplus*
Gunthorp	1913	Cowley, Douglas, & Jefferson cos., KS	Cowley probably *mundus,* others probably *birdi*
Brolemann	1915	None	*hispidipes*
Chamberlin	1918	Creston, Natchitoches, Par., LA	*birdi* and *amplus*
Attems	1938	IL and LA	IL = *hispidipes* LA = *amplus*
Chamberlin	1942a	Louisiana	*birdi* and *amplus*
Causey	1950a	Dixon Springs, Pope Co., IL	*oliphantus*
Causey	1952b	aperture drawing probably of Dixon Springs male	*oliphantus*
Chamberlin & Hoffman	1958	refer to IL in general and Dixon Springs	*hispidipes* and *oliphantus*
Stewart	1969	Angelina, Nacogdoches, Rusk, Shelby, Smith, Sabine, and Upshur, cos., TX	*amplus*

ponents are linked either through the aperture, gonopods, or both, and are thus more closely related to each other than to ones in other lineages. With 17 species this is the largest branch of *Eurymerodesmus,* extending from the Atlantic seaboard to southern Illinois, central Missouri, western Arkansas, and eastern Texas. For convenience, it is divided into four species groups based on gonopod structure. It contains the second oldest species in the family, *impurus,* and the type species of the genus-group names, *Kewanius* and *Paresmus.* Since the former has priority by four years and thus is available for future subgeneric designation, it is employed here to designate the lineage.

The **Impurus** Group

This group contains the four species of *Eurymerodesmus* with long acropodites, subequal to or only slightly shorter than the prefemora, or about 1/3 to 2/3 of the telopodite length. Since the acropodite is longer than in the other groups, the telopodite appears longer and typically extends beyond the level of the distal extremities of the hairs. The distal corners of the cyphopodal valves are moderately prolonged in *goodi* and extended into curved rigid dactyliform projections in *impurus* and *angularis. Eurymerodesmus compressus* has a shorter acropodite, around 3/8 of the telopodite length, but it belongs in this group because the structure is still longer than those of other groups and because its cyphopod valves are produced into long, tapered projections. That of the lateral valve is

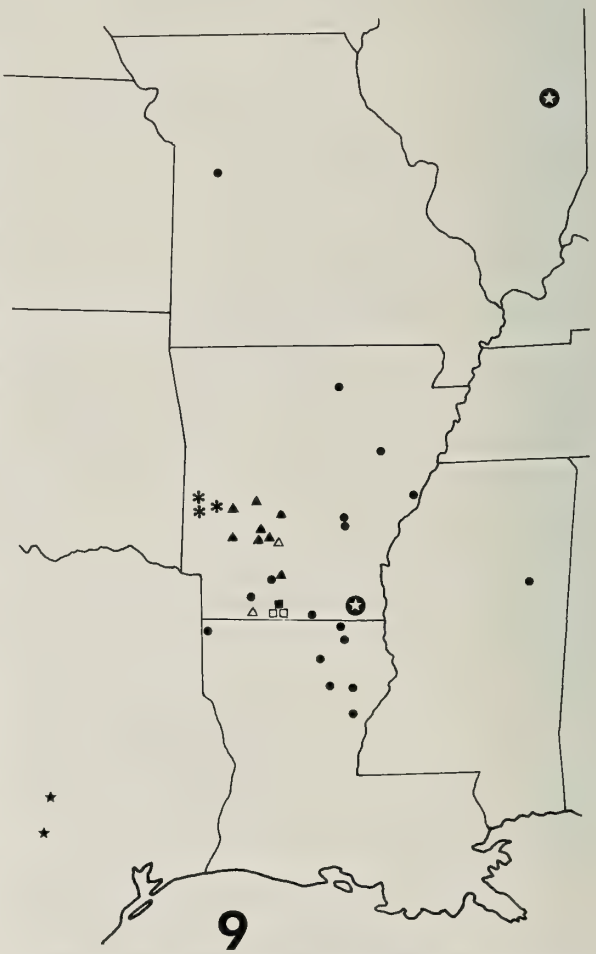


Fig. 9. Distributions of the *hispidipes* lineage, and the *impurus* and *dubius* groups. Stars in dots, *hispidipes;* stars, *impurus;* dots, *angularis;* squares, *compressus;* asterisks, *goodi;* triangles, *dubius.* Open squares and triangles denote literature records considered reliable.

longer, and that of the medial valve is closely appressed to its inner surface.

The *impurus* group occurs primarily in southern Arkansas and northern Louisiana, with outlying localities in central Missouri and north-central Mississippi. *Eurymerodesmus impurus* itself is allopatric, occurring some 240 miles to the southwest in eastern Texas adjacent to the *melacis* lineage. Additional forms with long acropodites may await discovery in northeast Texas.

Components. — *impurus* (Wood), *angularis* Causey, *compressus* Causey, *goodi* Causey.

Eurymerodesmus impurus (Wood), new combination
Figs. 9-16, 212

Polydesmus impurus Wood, 1867:43. Attems, 1940;493.
Leptodesmus impurus: Bollman, 1893:122.
Paresmus impurus: Causey, 1952a:174-175, figs. 8-9. Chamberlin and Hoffman, 1958:82.

Type specimens. — Two male syntypes (ANSP) collected by Gideon Lincecum on an unknown date in 1866 at Long Point, Washington Co., TX. The vial contains parts of two highly fragmented, incomplete males with two epiprocts, two gonopodal segments, but only one head. Both gonopods are missing from one gonopodal segment, and their location is unknown. The vial contains two labels with partly conflicting messages. One states "*Polydesmus impurus* Wood, type," and the other reads "*Leptodesmus impurus* Wood, probably type." There is a slide at the AMNH labeled "*Leptodesmus impurus* Wood, Dr. Lincecum, probably type, 1506 Phila. Acad.," which is empty but may have once contained the lost gonopods from the male at the ANSP. However, the number 1506 does not match those in the vial. The word "probably" on one label indicates some doubt that this is the type material of *impurus,* but it must be considered as such with no other specimens available.

Diagnosis. — A moderate-size species; males characterized by long mandibular projection; sides of aperture undivided, without true caudolateral pouches, elevating steeply and extending beyond caudolateral corner, inner surface concave thus forming false pouch; caudal margin flush with metazonal surface; telopodite long; acropodite very long, about 2/3 of telopodite length, broadly terminal, moderately demarcated from prefemur; latter with moderate number of hairs arranged continuously along inner margin; cyphopod valves of females with bowed projections from distal corners, apices touching or nearly so; receptacle large, sides curving partly around operculum.

Color in Life. — Peritremata reddish; metaterga light with darker mottled areas, with reddish stripes along caudal margins connecting paranotal markings; collum with reddish stripes along both anterior and posterior margins (Wood 1867).

Syntypes. — Bodies highly fragmented, lengths unmeasurable, maximum width 2.8 mm.

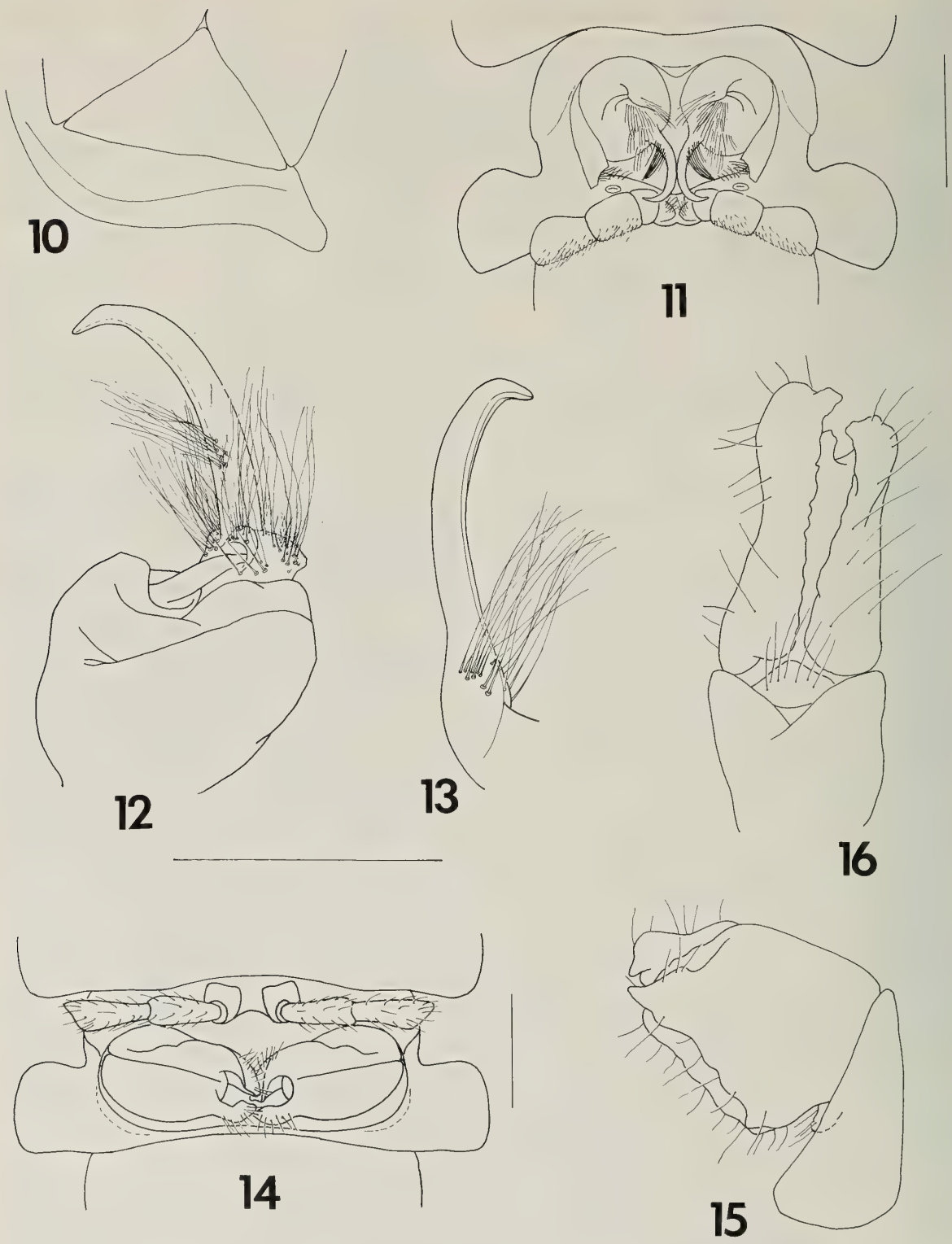
Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 1.6 mm, interantennal isthmus 0.4 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres 2>5>6>4>3>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, subantennal, frontal, and genal absent, clypeal about 8-8, labral about 14-14. Process of mandibular stipes relatively long, broadly rounded apically (Fig. 10).

Collum extending slightly below ends of following tergite. Paranota relatively flattened, interrupting slope of dorsum, posterior corners rounded to midbody segments, becoming blunt and progressively more acute thereafter.

5th and 6th sterna with low, rounded knob-like projections between both pairs of leg coxae, narrowly segregated in midline, caudal projections slightly larger than anterior ones on each segment. Postgonopodal sterna with two large, widely separated projections between 9th legs, lengths subequal to widths of adjacent coxae, with tuft of long hairs arising apically and from medial surface; remaining sterna without projections but with variable bicruciform impressions and hair patches adjacent to leg coxae, becoming flatter and more sparsely hirsute caudally. 2nd coxae with conical anterodistal projection, without caudal projection. Prefemoral lobes extending through segment 11.

Gonopodal aperture (Fig. 11) ovoid, without true caudolateral pouch but with concavity on inner surface of lateral flange, with moderate anterior indentation, 1.7 mm wide and 0.8 mm long at maxima, outline of entire apparatus rectangular; anterior indentation broadly rounded, triangular; sides not divided, elevating steeply in anterior half, leaning slightly over opening and continuing ventrad as laminate triangular flange, extending caudad beyond caudal margin, terminating abruptly, and dropping to metzonal surface beyond caudolateral corner, with shallow concavity on inner surface, rims essentially smooth; caudal margin flush with metazonal surface, discontinuous with sides, arising from inner surface of lateral flange, curving slightly caudad in midline; margins glabrous except for moderate hair tufts arising from inner surfaces of concavities of lateral flanges. Gonopods *in situ* (Fig. 11) with telopodites curving mediad, touching opposite member in midline, then curving laterad, extending beyond caudal margin of aperture and terminating over 9th coxae. Gonopod structure as follows (Figs. 12-13): Telopodite relatively long, extending just beyond level of distal extremities of hairs. Prefemur short, about 1/3 of telopodite length, terminating in slight swelling beyond ventral bend, with two rows of continuous, regularly spaced hairs along inner margin, distal tufts of 8-12 hairs on medial and lateral surfaces, and one medial hair at level of bend. Acropodite broadly terminal and very long, much longer than prefemur and about 2/3 of telopodite length, slightly narrower than distal extremity of prefemur, inner margin continuous with latter, outer margin curving inward slightly basally, leaning slightly over coxa but extending nearly directly caudad, expanding slightly



Figs. 10-16. *Eurymerodesmus impurus.* 10, right mandibular projection of male from Brazos Co., TX, lateral view. 11, aperture and gonopods *in situ* of holotype, ventral view. 12, left gonopod of the same, lateral view. 13, telopodite of the same, medial view. 14, cyphopods *in situ,* ventral view of female from Brazos Co., TX. 15, left cyphopod of the same, caudal view. 16, the same, medial view. Scale lines for figs. 11 and 14 = 1.00 mm. Line for other figs. = 0.60 mm for 10 and 15, 0.70 mm for 12 and 16, and 1.00 mm for 13.

then narrowing abruptly apically and bending sharply sublaterad, tip subacuminate.

Female from Brazos County, TX. — Length approximately 18.7 mm, maximum width 3.2 mm, W/L ratio 17.1%. Agreeing closely with types in somatic features, with following exceptions: Genal setae 3-3. Corner of mandibular stipes slightly produced, apically blunt. Sterna flat, unmodified, glabrous.

Cyphopodal aperture elliptical, sides strongly elevated above metazonal surface. Cyphopods *in situ* (Fig. 14) with valves extruded through aperture, almost completely exposed, oriented transversely, open side directed dorsad. Valves (Figs. 15-16) large, unequal, anterior valve larger, distal corners extending into broad, curved opposing projections, that of anterior valve broader, apically blunt, and directed subcaudad, that of caudal valve more acute, curving anteriad. Receptacle large, glabrous, located lateral to valves, extending well below latter, sides curving broadly mediad and partly enveloping operculum. Latter small, tucked under open (dorsal) side of valves.

Variation. — Measurements of a male from Brazos County are length 27.0 mm, maximum width 4.0 mm, W/L ratio 14.8%. Facial setae include frontal and subantennal series, 1-1 each. The apertures in these males are wider than those of the types, since the lateral flanges project directly ventrad or angle sublaterad instead of leaning over the opening. The apices of the flanges are squared rather than pointed, and a few scattered hairs arise from the anterior margin, the lateral rims, and the outer surfaces of the flanges. The apices of the acropodites curve more strongly than do those of the types.

Ecology. — According to Wood (1867), the types were collected under dried cow dung, hence the specific name. As noted by Causey (1952a), it is not unusual for millipeds to occur under dung in grassland ecosystems, where there is little other cover.

Distribution. — Known only from Washington and Brazos Counties, in the Coastal Plain of southeastern Texas (Figs. 9, 212). Material was examined as follows:

TEXAS: *Washington Co.,* Long Point, 2M, G. Lincecum (ANSP) TYPE LOCALITY. *Brazos Co.,* College Station, 2M, 4F, 23-24 December 1905, collector unknown (MCZ).

Remarks. — Wood's original description of *impurus* (1867) is internally contradictory about the gonopods. He mentions "two spines," the larger being regularly curved except apically, where it is abruptly bent. The smaller is "slender, curved, and acute." Since the telopodite is undivided, there is no prefemoral process, and the "larger" projection is clearly the telopodite, I surmise that Wood mistook one or more hairs as the second projection. Wood also contradicts himself regarding the distance that the hairs extend along the telopodite. He first states that the "blunt distal end is covered with long hairs," then mentions that neither of the "two spines" is hairy. Only with the present illustrations can this confusion be clarified. The prefemur of *impurus* is relatively short and the acropodite comparatively long; thus the telopodite does not appear as hairy as those in other species groups.

Causey (1952a) reported that Dr. Lincecum, a pioneer physician and Texas naturalist, traveled widely in the state, that it was impossible to determine the collecting site, and that his last home was "Bonham, Washington County." However, Bonham is in Fannin County, in north Texas adjacent to Oklahoma. The town in Washington County is Brenham, and one cannot determine whether her error is in the town or county. However, the Lincecum papers at the University of Texas library reveal that, in 1866, he or a few assistants collected all the Texas myriapods described by Wood (1867) at his home in Long Point, near Brenham (J. Reddell, pers. comm.). This site is therefore the type locality.

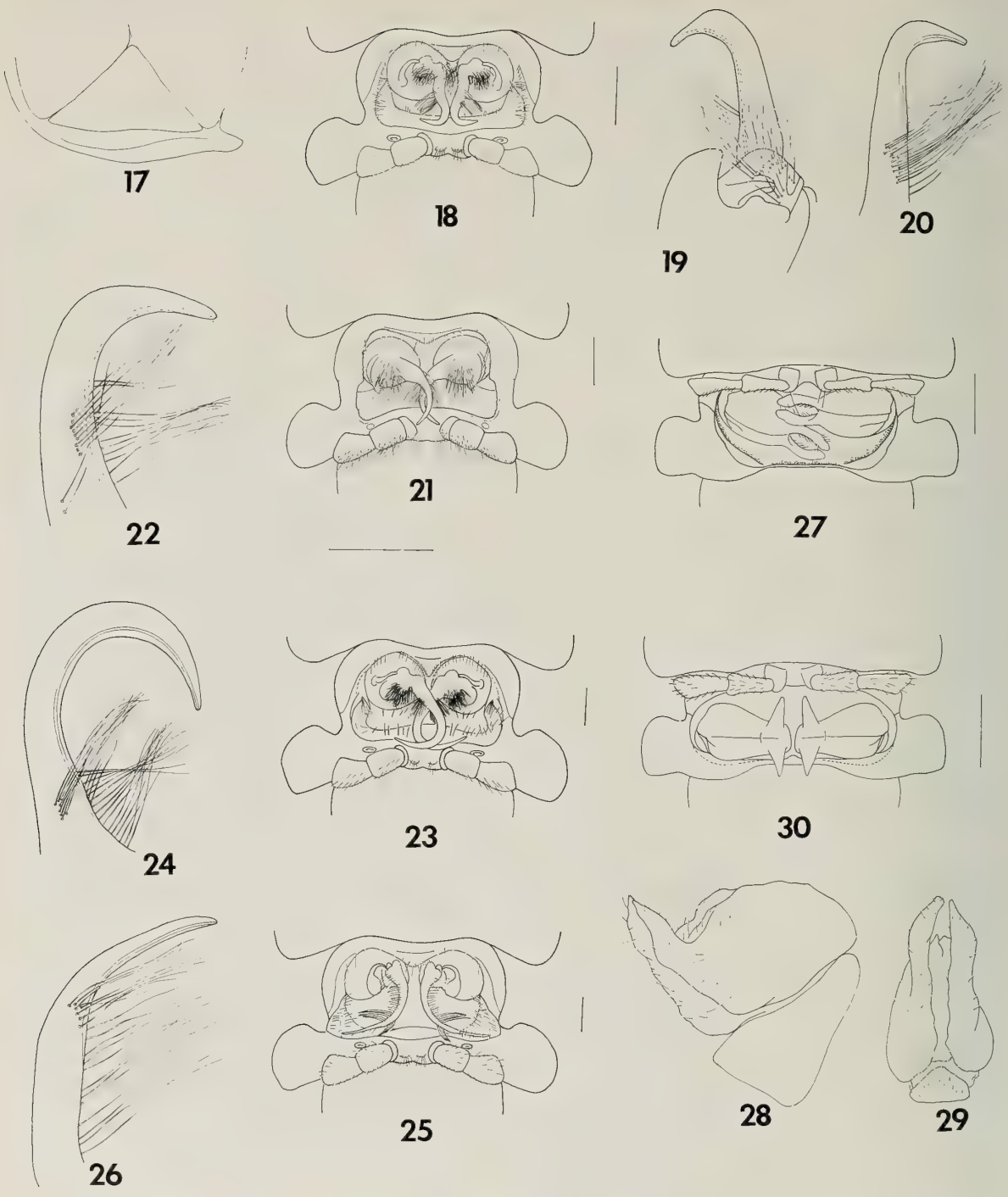
I visited Washington County in February 1986 to try to recollect *impurus* and verify the type locality. This effort was unsuccessful, but the samples from adjacent Brazos County confirm its occurrence in Washington County. Causey (1952a) reported that the types lacked gonopods, but they were present on one specimen when I examined them in 1987, so she did not thoroughly examine the sample. Her sketches of the aperture from ventral and lateral views, some 85 years after its description, were the first illustrations of *impurus,* but they do not adequately portray the size of the lateral flange. The gonopods were omitted since she overlooked them, so the long acropodites were previously unknown, although as stated above Wood (1867) alludes confusingly to this condition in the original description. Without illustration, it is not surprising that Causey did not deduce the nature of the telopodite. The virtual absence of meaningful illustrations of the four oldest referrable names — *hispidipes, impurus, varius,* and *simplex* — has greatly hampered identifications in *Eurymerodesmus* and use of these animals in other studies.

Eurymerodesmus angularis Causey
Figs. 9, 17-30, 211

Eurymerodesmus angularis Causey, 1951:69-71, figs. 1-3. Chamberlin and Hoffman, 1958:78.

Eurymerodesmus wellesleybentoni Causey, 1952a:171-174, fig. 5. **NEW SYNONYMY.**

Eurymerodesmus wellesleybentonus: Chamberlin and Hoffman, 1958:81.



Figs. 17-30. *Eurymerodesmus angularis*. 17, right mandibular projection of male from Jefferson Co., AR, lateral view. 18, aperture and gonopods *in situ* of the same, ventral view. 19, left gonopod of the same, lateral view. 20, telopodite of the same, medial view. 21, aperture and gonopods *in situ* of male from Phillips Co., AR, ventral view. 22, telopodite of left gonopod of the same, medial view. 23, aperture and gonopods *in situ* of male from Union Co., AR, ventral view. 24, telopodite of left gonopod of the same, medial view. 25, aperture and gonopods *in situ* of male from Caddo Par., LA, ventral view. 26, telopodite of left gonopod of the same, medial view. 27, cyphopods *in situ*, ventral view of female from Jefferson Co., AR. 28, left cyphopod of the same, caudal view. 29, the same dorsomedial view. 30, cyphopods *in situ*, ventral view of female from Ouachita Par., LA. Scale lines for figs. 18, 21, 23, 25, 27, and 30 = 1.00 mm. Line for other figs. = 0.30 mm for 17 and 28-29, and 0.50 mm for 19-20, 22, 24, and 26.

Type specimens. — Male holotype and female allotype (ANSP) collected by L. Gray, 1 April 1950, at DeValls Bluff, Prairie Co., AR. The allotype lacks the valvular projections found on females with other males of *angularis* and probably is not conspecific with the holotype. Consequently, a specimen from adjacent Jefferson County is used for the female description.

Diagnosis. — A large species; males characterized by short mandibular projection; sides of aperture divided, with variably open to closed caudolateral pouches; telopodite long; acropodite variably long, 1/3 to 3/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, curving gently to strongly dorsolaterad, configuration varying from obtuse angle to falcate; prefemur with moderate number of hairs arranged continuously along inner margin; cyphopod valves of females with dactyliform projections from distal corners, varying from bowed with apices touching or nearly so to linear and directed oppositely; receptacle large, sides curving partly around operculum.

Color in Life. — Paranota orange; metaterga dark mottled olive to black-brown, with or without orange stripes along caudal margins; collum with orange stripe along anterior margin (Causey 1951, 1952a).

Holotype. — Length 36.4 mm, maximum width 4.9 mm, W/L ratio 13.5%.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 3.0 mm, interantennal isthmus 1.0 mm. Antennae reaching back to midlength of 3rd tergite, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae with faint impressions. Facial setae as follows: epicranial 2-2, interantennal and genal absent, subantennal 1-1, frontal 1-1, clypeal about 11-11, labral about 23-23. Process of mandibular stipes short, broadly rounded (Fig. 17).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-11, becoming progressively more acute caudad.

5th sternum with low, sparsely hirsute, paramedian knobs between 4th legs and larger, more conical ones between 5th legs; 6th sternum with low, rounded, subequal knobs between 6th and 7th legs, each sparsely hirsute. Postgonopodal sterna with low, slightly hirsute lobes between 9th legs; segments 8-10 with minute, sparsely hirsute, paramedian knobs between anterior legs and larger, conical, sparsely hirsute knobs between caudal legs; remaining sterna with knobs between caudal legs becoming progressively shorter caudad, disappearing on segment 18. 2nd coxae with distinct, subconical anterodistal lobes and shorter, acute caudal ones. Prefemora with broad lobes on outer surfaces of all legs, becoming considerably smaller on caudalmost segments.

Gonopodal aperture (Fig. 18, not this specimen) broadly subovoid, with broad, open, caudolateral pouch and strong anterior indentation, 2.6 mm wide and 1.3 mm long at maxima, outline of apparatus subtrapezoidal, extending laterad well beyond stigmata and cephalad nearly to anterior segmental margin, severely constricting prozonum; anterior indentation broadly triangular; sides divided, angling slightly caudolaterad and becoming increasingly elevated to division point, inner lateral margin angling dorsad into opening then curving into inner caudal margin, outer lateral margin tapering gradually dorsad, flaring strongly laterad and curving broadly into blunt caudolateral corner, forming broad, deep, open pouch with inner lateral margin, rims smooth; inner caudolateral corner blunt; outer caudolateral corner blunt; inner caudal margin sublinear, subparallel to outer caudal margin; latter sloping to metazonum, curving gently along anterior surfaces to coxal condyles, extending slightly caudad between legs; margins irregularly hiruste with long hairs arising sporadically from anterior and lateral rims and outer surfaces and overhanging opening, also with moderate tufts of hairs in caudolateral pouches and scattered hairs along outer caudal margin. Gonopods *in situ* (Fig. 18, not this specimen) with telopodites extending caudoventrad from medial margins of coxae and touching in midline, apices curving dorsolaterad over caudal margins of aperture. Gonopod structure as follows (Figs. 19-20): Telopodite moderately long, terminating at level of distal extremities of hairs. Prefemur short, approximately 1/3 of telopodite length, tapering slightly distad into indistinct medial shoulder, with two rows of continuous, regularly arranged hairs along inner margin and dense distomedial tuft of around a dozen hairs. Acropodite long and broadly terminal, about 2/3 of telopodite length, continuous with, and poorly demarcated from, prefemur, curving dorsolaterad in about a right angle proximal to midlength, narrowing continuously to subacuminate tip.

Female from Jefferson Co. — Length 29.9 mm, maximum width 4.1 mm, W/L ratio 13.7%. Agreeing closely with holotype in somatic features, with following exceptions: Mandibular stipes with short, acuminate process. Sterna flat, unmodified, with hair tufts adjacent to leg coxae, becoming progressively sparser caudally.

Cyphopodal aperture ovoid, sides strongly elevated above metazonal surface, thickened. Cyphopods *in situ* (Fig. 27) with valves submerged and oriented transversely in aperture, valvular projections directed mediad and abutting or overlying each other in midline. Valves (Figs. 28-29) moderately large, subequal, corners extending into moderately long, dactyliform projections, curving toward each other and nearly touching apically. Receptacle large, located dorsolaterad to valves, corners curving partly around operculum. Latter small, located under free, dorsal, end of valves.

Variation. — I include under *angularis* all forms in Arkansas, Louisiana, and Mississippi with long acropodites, at least 1/3 of the length of the telopodite, that curve or bend by midlength and whose apertures display divided lateral margins with caudolateral pouches that vary from open to closed. The sides are entire and pouches are absent from *goodi,* whose acropodites curve apically. *Eurymerodesmus angularis* is highly variable in both sexes, and the only plausible alternative is several different species. The situation is analogous to that with the xystodesmid *Deltotaria brimleii brimleii* Causey in the southern Appalachian Mountains, where a host of dissimilar forms, none demonstrating structural stability over a broad geographical area, con-

nect through intermediate populations that bridge the anatomical gaps (Shelley and Whitehead 1986). Intervening forms are unknown in *angularis,* but future collections are expected to show that the localized forms blend together into a single taxonomic unit. A few, such as the falcate form in Union County, Arkansas, may warrant taxonomic recognition as subspecies, but these decisions are left to future investigators with access to more material. The name *wellesleybentoni* Causey (1952a), a cumbersome amalgam of the first and last names of the collector, was proposed for a form from Phillips County, Arkansas, with a stronger acropodal bend, and fortunately can be placed in synonymy.

Variation in males of *angularis* is analyzed geographically from the type locality, beginning with forms to the north and east and proceeding to the south and west. The males from Missouri are nearly identical to the holotypes, but that from Izard County, Arkansas, a partial specimen, is similar to the one from south of Strong, Union County, Arkansas in possessing a longer, strongly falcate acropodite, which is about 3/4 of the telopodite length. The outer lateral margin in the Izard County male is lower than the anterior part of the side and does not extend as far laterad thus forming a shallower pouch.

East of the type locality there is a trend toward shorter acropodites beginning with the form named *wellesleybentoni* from Phillips County, where it is subequal to the prefemur and bends more strongly dorsolaterad near midlength (Fig. 22). The outer lateral margin is the same elevation and nearly linear with the anterior part of the sides, and since the inner lateral margin curves, the pouch is comparatively narrow, shallow, and closed (Fig. 21). Farther east in Oktibbeha County, Mississippi, the acropodite is subequal to the prefemur and curves slightly dorsolaterad. The outer lateral margin is lower than the anterior part of the sides and flares moderately laterad, thus forming a moderate, partly open pouch.

Forms south of the type locality exhibit greater variability in both the gonopods and apertures, although those from adjacent Jefferson County closely resemble the types. The acropodites and prefemora are subequal in length in all north-central Louisiana males except those from Ouachita Parish, where the former is much shorter, about 1/3 of the telopodite length and resembles the condition in *compressus.* The acropodite curves slightly dorsolaterad in Morehouse Parish and more directly laterad in the Franklin and Catahoula males. The outer lateral margin slopes dorsad and flares farther laterad in these specimens thus forming a larger pouch.

Three forms occur in Union County, Arkansas. The males south of Strong display long falcate acropodites, around 3/4 of the telopodite length (Fig. 24), that are convergent with the variant in Izard County. The bases of the acropodites cross in the midline, then they curl over the outer caudal margin on the opposite side of the aperture and cross the midline and the opposite member again over the sternum between the 9th legs. The outer lateral margin rises from the division point, and the inner lateral margin extends well into the opening, thus forming a deep, open pouch (Fig. 23). The precise locality of the other Union County form is unknown, but the acropodite comprises about half the telopodite length and curves nearly directly dorsad over the sternum between the 9th legs; the prefemur exhibits a distinct distomedial shoulder. The outer lateral margin is level, flares moderately laterad, and forms a moderate pouch with the inner margin.

Forms in southwestern Arkansas and adjacent Louisiana display moderately long acropodites. Those from Columbia County, Arkansas, are subequal to the prefemur, or 1/2 of the telopodite length, and curve distinctly laterad; there is a slight distal shoulder on the prefemur. The outer lateral margin flares farther laterad, and the inner margin curves more into the opening, thus forming a broader and deeper pouch. The Caddo Parish, Louisiana, male has a very long, bisinuate acropodite, but it is only about half the telopodite length because the prefemur is also longer (Figs. 25-26). The telopodite curves strongly laterad, extending into the pouch, and the outer lateral margin is much higher than the anterior parts of the sides. The inner margin curves smoothly into the opening and the inner caudal margin (Fig. 25).

Less can be said about variation in females because most samples contain only males. Females from Franklin and Catahoula Parishes, Louisiana, resemble those from Jefferson County, Arkansas, in having subequal dactyliform projections from the valves that are bowed towards each other and touch in some individuals, thus resembling opposable digits or claspers. The projections are shorter and diverge, extending directly anteriad and caudad, in the female from Ouachita Parish, Louisiana (Fig. 30).

Ecology. — No habitat comments have appeared in the literature, and the only notation on sample

labels is "leaf mold in woodland" for the sample from Jefferson County, Arkansas.

Distribution. — The Coastal Plain of Arkansas and northern Louisiana, extending eastward to eastern Mississippi and northward in Missouri to the fringe of the Ouachita Physiographic Province (Figs. 9, 211). Specimens were examined as follows:

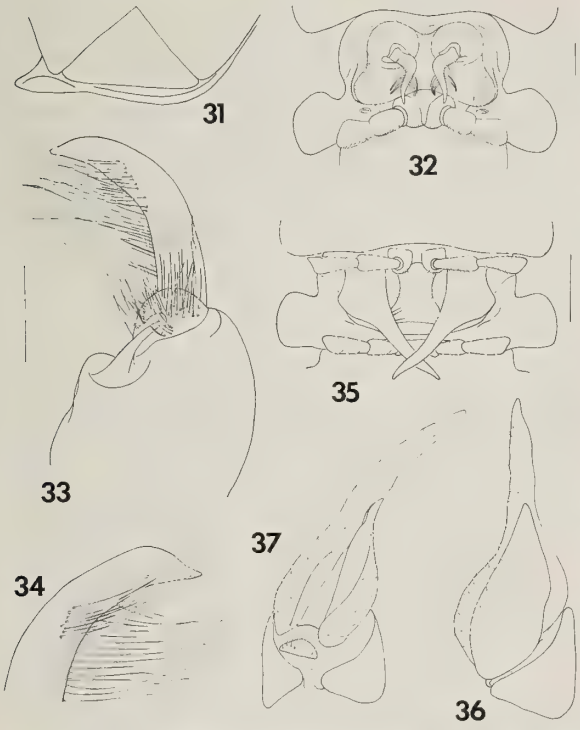
MISSOURI: *Johnson Co.,* Warrensburg, 2M, 2F, 8 April 1962, K. Oyer (FSCA).

ARKANSAS: *Izard Co.,* Mt. Pleasant, M, 23 December 1954, N. B. Causey (FSCA). *Prairie Co.,* DeValls Bluff, M, F, 1 April 1950, L. Gray (ANSP) TYPE LOCALITY. *Jefferson Co.,* 0.5 mi. S. Altheimer, west of AR hwy. 88, 5M, 3F, 14 April 1956, collector unknown (FSCA). *Phillips Co.,* Helena, M, October-November 1951, W. Benton (ANSP), and 20 mi. E Pine Bluff, M, F, October 1954, Kirkwood (FSCA). *Ouachita Co.,* 5 mi. SW Camden, M, F, 1 January 1956, A. B. Jones (FSCA). *Union Co.,* locality unknown, 3M, 8 January 1958, L. O. Warren (FSCA); and south of Strong, 3M, 19 March 1953, collector unknown (FSCA). *Columbia Co.,* Magnolia, 4M, 28 January 1955, P. Waler (FSCA), M, 19 April 1958, W. F. Evans (FSCA), and 2M, 26 November 1961, R. Rogers (FSCA).

LOUISIANA: *Caddo Par.,* ca. 30 mi. NNW Shreveport, near Myrtis on McCloud-State Line Rd., 0.3 mi. W LA hwy. 1, M, 11 March 1966, R. E. Tandy (FSCA). *Morehouse Par.,* 12 mi. N Bastrop, along LA hwy. 142, 2.1 mi. S AR line, M, 16 March 1967, J. E. and M. R. Cooper (NCSM); and 5 mi. S Mer Rouge, M, F, 24 December 1954, N. B. Causey (FSCA). *Ouachita Par.,* Monroe, 4M, 2 April 1969, collector unknown (FSCA), and 1410 Forsyth Ave, M, 26 April 1976, and F, 31 December 1974, M. R. and J. E. Cooper (NCSM). *Caldwell Par.,* along Lafourche River, 3M, F, date and collector unknown (FSCA). *Franklin Par.,* Winnsboro, M, F, May 1953, M. K. Wiggers (FSCA). *Catahoula Par.,* ca. 17 mi. NE Jonesville, along LA hwy. 15 between Peck and Sicily Island, 3M, 3F, 24 December 1954, N. B. Causey (FSCA); and 4 mi. W Sicily Island, along LA hwy, 8, F, date unknown, R. E. Tandy (FSCA).

MISSISSIPPI: *Oktibbeha Co.,* Craig Springs, M, 22 April 1980, G. Snodgrass (MEM, NCSM).

Remarks. — With known occurrence in the western fringe of Caddo Parish, Louisiana, *angularis* should be expected in Cass and Marion counties, Texas.



Figs. 31-37. *Eurymerodesmus compressus.* 31, left mandibular projection of neotype, lateral view. 32, aperture and gonopods *in situ* of neotype, ventral view. 33, left gonopod of the same, lateral view. 34, telopodite of the same, medial view. 35, cyphopods *in situ,* ventral view of female from Union Co., AR. 36, left cyphopod of the same, medial view. 37, the same, caudal view. Scale lines for figs. 32 and 35 = 1.00 mm. Line for other figs. = 0.25 mm for 36-37, 0.30 mm for 31, 0.40 mm for 33, and 0.50 mm for 34.

Eurymerodesmus compressus Causey
Figs. 9, 31-37, 211

Eurymerodesmus compressus Causey, 1952a:169-171, figs. 1-4. Chamberlin and Hoffman, 1958:79.

Type specimen. — Male neotype and one associated female (FSCA) collected by W. Nesbit on an unspecified date in 1957, 6 mi. W El Dorado, Union Co., AR. This site is about 4 mi. N of the type locality, Junction City, Union County, where 16 males and 2 females were collected in October 1950. The types are missing from the ANSP, the published repository (Causey 1952a, Chamberlin and Hoffman (1958), nor is there any material from Junction City in the FSCA. According to Causey (1952a), 1 female topotype was collected at Junction City on 10 May 1950 and 11 males were taken there on 16 January 1952.

Diagnosis. — A large species; males characterized by long mandibular projection; sides of aperture divided, with open caudolateral pouches; telopodite moderately long; acropodite moderately long, about

3/8 of telopodite length, broadly terminal, poorly demarcated from prefemur, laterally compressed; prefemur with many hairs arranged continuously along inner margin; cyphopod valves of females with unequal, closely appressed, rigid projections from distal corners, that of outer (lateral) valve very long, dactyliform, overhanging at least segment 4 *in situ,* that of inner (medial) valve much shorter, subtriangular; receptacle moderately large, sides curving partly around operculum.

Color in life. — Peritremata orange: metaterga uniformly dark mottled olive, without stripes; collum with orange stripe along anterior margin (Causey 1952a).

Neotype. — Length 37.4 mm, maximum width 5.4 mm, W/L ratio 14.4%

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 3.1 mm, interantennal isthmus 1.0 mm. Antennae reaching back to anterior half of 3rd tergite, relative lengths of antennomeres 2>3>5>4=6>1>7. Genae with faint impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, subantennal 1-1, clypeal about 14-14, labral about 20-20. Process of mandibular stipes (Fig. 31) moderately long and broad, apically blunt and rounded.

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-10, becoming progressively more acute caudad.

5th sternum with low, sparsely hirsute areas between 4th legs, narrowly segregated in midline, and strong, sparsely hirsute projections between 5th legs, narrowly segregated in midline; 6th sternum with low, sparsely hirsute elevated areas between both leg pairs, widely separated in midline, those between anterior (6th) legs higher. Postgonopodal sterna with deep central impression between 9th legs; segments 8-9 with low, knob-like projections between both leg pairs, narrowly segregated in midline, those between caudal legs much higher with a few more hairs; segments 10-15 flat between anterior legs, with moderate knob-like projections between caudal legs, becoming progressively smaller caudally with only light hirsute patches on segments 16-18. 2nd coxae with sharply conical anterodistal lobes, caudal lobes absent. Prefemoral lobes present on all legs, becoming smaller on caudalmost segments.

Gonopodal aperture (Fig. 32) broadly trapezoidal, with narrow, open caudolateral pouches and broad anterior indentation, 2.9 mm wide and 1.3 mm long at maxima, outline of apparatus trapezoidal; anterior indentation short, broad, apically rounded; sides divided, angling slightly caudolaterad, elevating just beyond anterolateral corner and continuing to division point at midlength, inner lateral margin plunging deeply into opening then curving broadly into inner caudal margin, outer lateral margin tapering rapidly dorsad, flaring slightly laterad and curving into outer caudolateral corner, forming narrow, open pouch with inner margin, rims essentially smooth; inner caudolateral corner smoothly rounded; outer caudolateral corner generally broadly rounded, somewhat irregular; inner caudal margin curving anteriad, parallel to outer caudal margin; latter curving broadly anteriad along anterior surfaces of coxal condyles; margins irregularly hirsute with long hairs arising from rims and outer surfaces of sides, slightly more hairs on anterior indentation and moderately dense tufts from pouches, caudal margins glabrous. Gonopods *in situ* (Fig. 32) with telopodites extending caudad in subparallel arrangement, continuing beyond caudal margins of aperture and terminating over coxal condyles, apices directed dorsad. Gonopod structure as follows (Figs. 33-34): Telopodite moderately long, terminating well before distal extremities of hairs. Prefemur moderately long, about 5/8 of telopodite length, curving slightly near midlength and leaning over coxa, margins parallel, not tapering, without distal lobe or swelling, with two rows of long hairs along inner surface angling slightly outward, and distomedial tuft of 8-10 hairs. Acropodite moderately long and broadly terminal, about 3/8 of telopodite length, continuous with, and poorly demarcated from, prefemur, compressed laterally, curving slightly more dorsad, sides tapering rapidly beyond midlength to subacuminate tip.

Female — Length 29.6 mm, maximum width 4.5 mm, W/L ratio 15.2%. Agreeing essentially with neotype in somatic features, with following exceptions: Mandibular stipes with short, acuminate, lightly sclerotized projection. Sterna flat, unmodified, with variably impressed transverse grooves originating between leg pairs and at most only a few scattered hairs per segment adjacent to caudal coxae.

Cyphopodal aperture elliptical, sides thickened, strongly elevated above metazonal surface, tapering rapidly to metazonum on caudal margin. Cyphopods *in situ* (Fig. 35) lying obliquely in aperture, open side anteromediad, valvular projections directed caudomediad over caudal margin of aperture, those of outer valves extending over sternum of segment 4, crossing in midline, terminating over prozonum of segment 5. Valves (Figs. 36-37) relatively large, unequal, lateral (outer) valve much larger, situated obliquely on receptacle, inner margins moderately hirsute, outer corners extended into unequal projections, that of inner valve relatively short and subtriangular, closely appressed to inner margin of outer valvular projection, latter very long, more than twice as long as inner projection, rigid, and digitiform, apically acuminate. Receptacle moderately large, glabrous, oriented dorsoventrally in aperture, sides curving broadly around sides of operculum. Latter small, situated directly beneath valves.

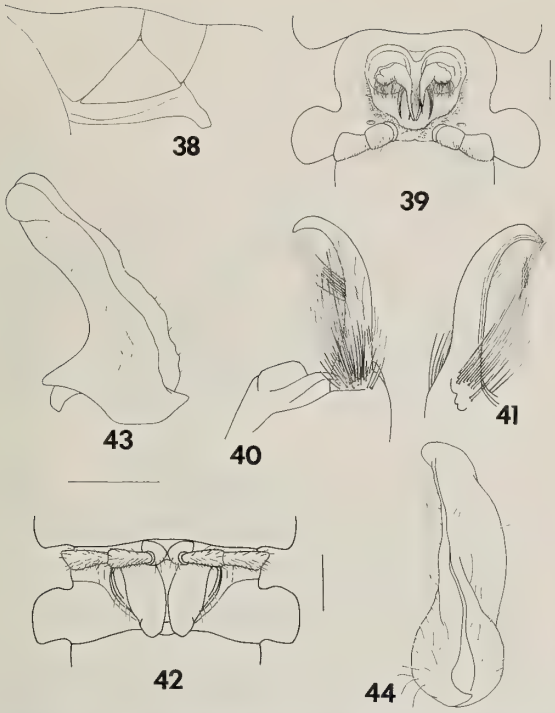
Ecology. — Unknown.

Distribution. — Known only from western Union County, Arkansas (Figs. 9, 211). In addition to Junction City, Causey (1952a) reported a female from Three Creeks, which is also lost. Thus, the neotype and female were the only specimens examined.

Remarks. — With a moderately long acropodite, 3/8 of the telopodite length, *compressus* spans the anatomical gap between the long structures displayed by the rest of the *impurus* group and the short ones, 1/4 of the telopodite length or less, found in the *varius* group, thus blending the dissimilar forms of these groups into one lineage.

Eurymerodesmus goodi Causey
Figs. 9, 38-44, 211

Eurymerodesmus goodi Causey, 1952b:3-4, fig. 1. Chamberlin and Hoffman, 1958:79-80.



Figs. 38-44. *Eurymerodesmus goodi.* 38, right mandibular projection of holotype, lateral view. 39, aperture and gonopods *in situ* of male from Montgomery Co., AR, ventral view. 40, left gonopod of holotype, lateral view. 41, telopodite of the same, medial view. 42, cyphopods *in situ,* ventral view of female from Polk Co., AR. 43, left cyphopod of the same, subcaudal view. 44, the same, anterolateral view. Scale lines for figs. 39 and 42 = 1.00 mm. Line for other figs. = 0.30 mm for 38 and 43-44, and 0.50 mm for 40-41.

Type specimen. — Male holotype (AMNH) collected by N. B. Causey, 7 September 1950, along Bard Springs Rd., 16 mi. SE Mena, Polk Co., AR.

Diagnosis. — A large species; males characterized by long mandibular projection; sides of aperture undivided, without caudolateral pouches, elevating slowly throughout, without modifications; telopodite long; acropodite long, about 2/3 of telopodite length, broadly terminal, moderately demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners extending into long, broad projections; receptacle absent.

Color in life. — Pertriemata reddish-orange; dorsum olive, darker on prozonites, lighter on metazonites; without metatergal stripes (Causey 1952b).

Holotype. — Body fragmented, length unmeasurable, maximum width 5.8 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 3.7 mm, interantennal isthmus 1.1 mm. Antennae reaching back to middle of 3rd tergite, relative lengths of antennomeres 2>5>4=6>3>1>7. Genae without impressions. Facial setae as follows: epicranial absent, interantennal 1-1, frontal 1-1, genal absent, clypeal about 11-11, labral about 20-20. Process of mandibular stipes long, angling caudad, apically blunt (Fig. 38).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded on anterior half of body, becoming blunt and progressively more acute on caudalmost segments.

5th sternum with short broad knob-like projections between both leg pairs; 6th sternum with broader, flatter elevated areas between both pairs of coxae. Postgonopodal sterna with slightly elevated, flattened areas between 9th legs; remaining sterna with hirsute, elevated areas on segments 8-10, becoming progressively flatter and less hirsute caudad, with incomplete transverse impressions originating between leg coxae. 2nd coxae with broad, truncate anterodistal lobe and shorter, acute caudal one. Prefemoral lobes present on all legs, becoming smaller on caudalmost segments.

Gonopodal aperture (Fig. 39, not this specimen) very wide, broadly ovoid, without caudolateral pouches, strongly indented anteriad at midline, 3.6 mm wide and 1.7 mm long at maxima; anterior indentation strong, broadly rounded; sides not divided, curving mediad caudally, elevation beginning behind anterolateral corner, continuing to peak at caudolateral corner, rims essentially smooth; caudolateral corner broadly rounded, obtuse; caudal margin continuous with sides at caudolateral corners, dropping abruptly to metazonal surface and continuing across midline; anterior margin glabrous, hairs beginning on sides behind anterolateral corners, becoming progressively denser caudad, arising from rim or slight distance down outer surface, densest at caudolateral corners, continuing along midline of caudal margin in linear arrangement. Gonopods *in situ* (Fig. 39, not this specimen) with telopodite angling caudomediad, apices nearly touching, located wholly within aperture. Gonopod structure as follows (Figs. 40-41): Telopodite relatively long, terminating before level of distal extremities of hairs. Prefemur short, about 1/3 of telopodite length, expanding distad and terminating in swollen area, with two rows of hairs along inner margin and distomedial tuft of about a dozen hairs. Acropodite long and broadly terminal, about 2/3 of telopodite length, moderately demarcated from prefemur, linear for most of length, curving broadly distal to midlength, sides tapering gradually then more rapidly apically, tip subacuminate.

Female from Polk Co. — Length 29.6 mm, maximum width 4.8 mm, W/L ratio 16.2%. Agreeing closely with holotype in somatic features, with following exceptions: Genal setae 1-1. Process of mandibular stipes short, blunt. Sterna relatively flat and unmodified, with faint, incomplete transverse impressions originating between coxae and at most only a few randomly scattered setae, especially along caudal margins.

Cyphopodal aperture ovoid, caudal margin extending caudad in midline, sides and caudal margin distinctly elevated above metazonal surface, caudal margin strongly flared, overhanging segment margin. Cyphopods *in situ* (Fig. 42) with ventral extensions of valves protruding through aperture, directed caudad, overhanging caudal margin of aperture and coxae of 3rd legs, open side visible, facing sublaterad. Valves (Figs. 43-44) large, moderately hirsute, slightly unequal, dorsal one with short, broad process curving over opening between valves, distal corners extending into long broad projections, longer than main part of valves, leaning dorsad, narrowing then expanding into rounded, knob-like termini. Receptacle absent. Operculum minute, tucked under anterior side of valves.

Variation. — Measurements of the male from Montgomery County illustrated in Figs. 39-41 are 32.5 mm in length, 5.3 mm in width, W/L ratio 16.3%. Its gonopods agree closely with those of the holotype, but the caudal aperture margin extends caudad between the 8th legs to near the sternal elevations.

Ecology. — Unknown.

Distribution. — Known only from southwestern Polk and southwestern Montgomery counties, Arkansas, in the southern fringe of the Ouachita Physiographic Province (Figs. 9, 211). Specimens were examined as follows:

ARKANSAS: *Polk Co.,* along Bard Springs Rd., 16 mi. SE Mena, M, 7 September 1950, N. B. Causey (AMNH) TYPE LOCALITY; and Shady Lake Rec. Area, M, F, 18 June 1953, D. Dowling (FSCA). *Montgomery Co.,* 10 mi. NW Langley (in Polk Co.), Albert Pike Cpgd., M, F, 1979, H. W. Robison (NCSM) and M, 24 December 1982, H. W. Robinson (NCSM).

Remarks. — *Eurymerodesmus goodi* is a relatively soft, flexible eurymerodesmid, and its large size is equivalent to that of moderately-large xystodesmids such as *Boraria profuga* (Causey), also occurring in Arkansas. Because of its size *goodi* is particularly likely to be misassigned to the Xystodesmidae, and close attention should be paid to the structures of the mandibular stipes and leg prefemora when making determinations.

The **Dubius** Group

Eurymerodesmus dubius shares a wide aperture lacking caudolateral pouches with *goodi,* which is parapatric on the north. It differs in having a short acropodite and short, mostly linear telopodites, the latter distinguishing it from other members of the *Kewanius* lineage. It differs from the species of the *varius* group in the linear telopodite and the absence of caudolateral pouches, and is distinguished from those in the *simplex* group by its broadly terminal acropodite.

Component. — *dubius* Chamberlin.

Eurymerodesmus dubius Chamberlin
Figs. 9, 45-53, 211

Eurymerodesmus dubius Chamberlin, 1943:38, fig. 8; 1952:573. Causey, 1952b:2-3. Chamberlin and Hoffman, 1958:79.

Paresmus columbus Causey, 1950a:272, figs. 10-11. Chamberlin and Hoffman, 1958:82. **NEW SYNONYMY.**

Type specimens. — Male holotype and female paratype (FMNH) collected by K. P. Schmidt, 16 April 1941, at Delight, Pike Co., AR.

Diagnosis. — A large species; males characterized by short mandibular projection; sides of aperture undivided, without caudolateral pouches, elevating slowly, without modifications; telopodite short, nearly upright for most of length; acropodite short, 1/8 to 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, gently curved; prefemur with many hairs arranged continuously along inner surface; cyphopod valves of females with distal corners only slightly extended; receptacle absent.

Color in life. — Unknown. Chamberlin's description (1943) indicates a stripe across the caudal margins of the metaterga, but the living colors cannot be inferred from those in preservative.

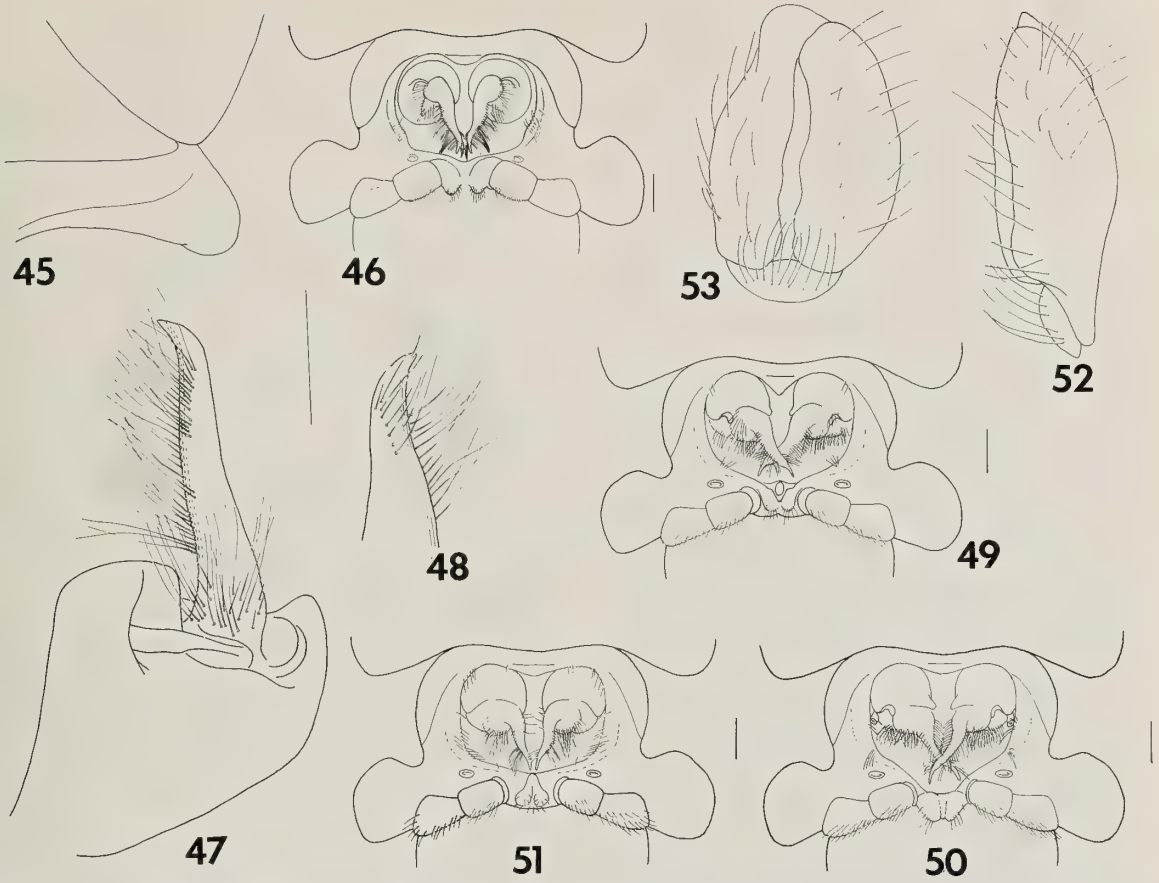
Holotype. — Body highly fragmented, length unmeasurable, maximum width 5.8 mm.

Somatic features similar to *hispidies,* with following exceptions: Width across genal apices 3.6 mm, interantennal isthmus 1.0 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>6>3=4=5>1>7. Genae with distinct, central impressions. Facial setae as follows: epicranial, interantennal, and frontal absent; genal 1-1, clypeal about 9-9, labral about 16-16. Process of mandibular stipes short and stout, apically broadly rounded (Fig. 45).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-14, becoming progressively more acute caudally.

5th sternum with short projections between anterior legs, closely appressed in midline, and broader, more widely segregated, knob-like processes between caudal legs; 6th sternum with short, knob-like projections between anterior legs and broad, flattened, areas between caudal legs. Postgonopodal sterna with short, broad lobes between 9th legs; sternum of segment 8 deeply incised transversely, with hair patches adjacent to leg coxae; remaining sterna becoming flatter and more plate-like caudally, with hair patches adjacent to leg coxae through segment 17, becoming progressively less hirsute caudad. 2nd coxae with short distal lobes on anterior and caudal surfaces. Prefemoral lobes extending through segment 12.

Gonopodal aperture (Fig. 46) nearly circular, without caudolateral pouches, with slight anterior indentation, 2.0 mm wide and 1.4 mm long at maxima; anterior indentation short and broad, apically rounded; sides curving gently caudomediad, undivided, elevating slightly to peak just before caudolateral corner, then dropping abruptly to metazonal surface, rims becoming slightly irregular caudad; caudolateral corner moderately blunt, sloping downward to metazonal surface; caudal margin not continuous with and much lower than lateral, extending slightly caudad in midline; anterior and caudal margins glabrous, sides with only a few scattered hairs on rim and outer surface near peak at caudolateral corners. Gonopods *in situ* (Fig. 46) angling toward midline with tips nearly touching, telopodites located wholly over aperture. Gonopod structure as follows (Figs. 47-48): Telopodite relatively short and upright, terminating well before level of distal extremities of hairs. Prefemur relatively long, about 7/8 of



Figs. 45-53. *Eurymerodesmus dubius*. 45, right mandibular projection of holotype, lateral view. 46, aperture and gonopods *in situ* of holotype, ventral view. 47, left gonopod of the same, lateral view. 48, telopodite of the same, medial view. 49, aperture and gonopods *in situ* of male from Bradley Co., AR, ventral view. 50-51, apertures and gonopods *in situ,* ventral views of two males from Clark Co., AR. 52, left cyphopod of female paratype, medial view. 53, the same, anterior view. Scale lines for figs. 46 and 49-51 = 1.00 mm. Line for other figs. = 0.35 mm for 45, 0.40 mm for 47, and 0.50 mm for 48 and 52-53.

telopodite length, upright but not linear, margins slightly bisinuately curved, narrowing slightly distad, basal hairs relatively sparse, hairs denser on stem, with two rows along inner margin angling outward distad and terminating in tuft of about 12 hairs, with distomedial tuft of 8 hairs. Acropodite very short, broadly terminal, about 1/8 of telopodite length, covered by prefemoral hairs, essentially just a short spur on distal extremity of prefemur, continuous with, and poorly demarcated from, latter, curving gently dorsad, sides tapering to acuminate tip.

Female paratype. — Body fragmented, length unmeasurable, maximum width 4.8 mm. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal and frontal setae present, 1-1 each; genal setae absent. Process of mandibular stipes indistinct, broadly rounded. Sterna relatively flat, unmodified, with at most only a few randomly scattered hairs on caudal margins.

Cyphopodal aperture small, circular, sides and caudal margin nearly flush with metazonal surface. Cyphopods *in situ* with tips of valves visible in aperture, not protruding, open side directed anteriad. Valves (Figs. 52-53) moderate-size, moderately hirsute, slightly unequal, outer (lateral) valve larger, distal corners very slightly extended, broadly rounded. Receptacle absent. Operculum relatively large, moderately hirsute, located at bases of valves on open (anterior) side.

Variation. — *Eurymerodesmus dubius* is one of the more flexible eurymerodesmids, and it was possible to uncoil without breakage and measure males from the counties in Table 4:

Table 4. Size variation of *E. dubius* males.

County	length	width	W/L ratio
Saline	37.8	6.4	1.69%
Garland	33.6	5.6	16.7%
Garland	33.6	5.6	16.7%
Montgomery	32.5	5.3	16.3%
Clark	25.0	4.7	18.8%
Clark	32.7	4.7	14.4%
Pike	34.3	5.5	16.0%
Pike	30.8	4.7	15.3%
Pike	33.6	5.6	16.7%
Pike	29.3	5.3	18.1%
Pike	31.6	5.5	17.4%
Pike	29.8	4.9	16.4%
Nevada	27.5	4.8	17.5%
Bradley	32.5	6.4	19.7%

Aside from one male from Clark County that lacks the distomedial tuft of prefemoral hairs, the gonopods of *dubius* are uniform. However, the *in situ* configuration varies depending upon the degree of coiling of the body, the degree to which the coxae are submerged under the lateral margins of the aperture, and the caudal configuration of the latter. Thus, the apices of the telopodites may be very close, touch, or cross, and they may be wholly within the aperture or slightly overlap the caudal rim. In one tightly coiled male, the aperture was nearly completely covered by segment 6, and the telopodites were correspondingly reoriented, being directed mediad with the apices extending across the opposite side of the aperture and the tips touching the opposing coxae.

As discussed by Causey (1952b), the aperture configuration and the size and shape of the sternal process(es) between the 9th legs vary considerably. The height and length of the lateral elevations varies, and they may be nearly linear or broadly curved. In northern populations, the lateral elevations extend around the caudolateral corners onto the caudal margin, where they terminate either abruptly or smoothly by tapering to the metazonal surface. However, in the southernmost populations from Nevada, Ouachita, and Bradley counties, the elevations are limited to the sides, terminating either at or just before the caudolateral corners.

The caudal margin displays two configurations. It is essentially straight as in the holotype in males from Saline, Garland, and Nevada counties, and in these individuals, the sternal projections between the 9th legs are separate, short, and knob-like, terminating well below the margins of the adjacent coxae. However, in some males from Montgomery, Clark, Pike, Ouachita, and Bradley counties, the margin extends caudad in the midline between the 9th legs terminating at, and tapering into, the sternal projection (Figs. 49-50). Coupled with the anterior indentation, the aperture in these individuals appears heart-shaped. In specimens from Montgomery, Pike, and Bradley counties, the sternal knobs are shorter than the adjacent coxal widths and are separated to varying degrees, either directed ventrad or leaning slightly toward the midline. However, in males from Clark and Ouachita counties, the knobs are coalesced in the midline to form a single ventral projection of varying length (Figs. 50-51). It is longer than the adjacent coxal widths in one male from Clark County (Fig. 50). As a further complication, a short midcaudal spur extends anteriad inside the aperture in a few males from Ouachita and Bradley counties (Fig. 49). None of these variants demonstrates enough consistency or enough of a geographical component to warrant taxonomic recognition at the subspecific level. However, they emphasize the need to examine every specimen; males within some samples differ.

The cyphopods generally resemble those of the female paratype and protrude through the aperture in a few individuals. In one from Garland County, the valves are oriented laterad/mediad, with the open side facing forward.

Ecology. — Labels with specimens from Bradley County state that they were taken in "large traps" in pine-oak woods.

Distribution. — The southern fringe of the Ouachita and the adjacent Coastal Plain Physiographic Provinces of southern Arkansas, with an allopatric record from Louisiana (Figs. 9, 211). Specimens were examined as follows:

ARKANSAS: *Montgomery Co.,* along US hwy. 270, 5.4 mi. E Mt. Ida, M, 6 March 1977, R. E. Woodruff (FSCA). *Garland Co.,* Hot Springs, 3M, F, 4 January 1957, collector unknown (FSCA); and Big Goat Island, Lake Hamilton, M, 28 December 1954, Atkins (FSCA). *Hot Springs Co.,* Magnet, F, 1880's but exact date unknown, Hutcherson (NMNH). *Saline Co.,* locality unknown, 2M, 2 juvs., 1950, N. B. Causey (FSCA). *Clark Co.,* 4.5 mi. N Arkadelphia, M, 19 January 1953, and 4M, February 1953, J. E. Sublette (FSCA); 4 mi. E Arkadelphia, M, F, date and collector unknown (FSCA); and 8 mi. W Arkadelphia, 3M, 2F, 10 September 1950, collector unknown (FSCA). *Pike Co.,* Delight, M, F, 16 April 1941, K. P. Schmidt (FMNH) TYPE LOCALITY; and Bear Cr., 7M, 2F, 18 April 1954, N. B. Causey (FSCA). *Nevada Co.,* Jackson Twp., 5M, 3F, 30 December 1954, R. Delaney (FSCA). *Ouachita Co.,* 5 mi. SW Camden, M, 27 November 1955, A. B. Jones (FSCA). *Bradley Co.,* Prospect, 3M, 29 November 1967, Whitcomb (FSCA); and Sumpter, 2F, September and 13 October 1965, and 3M, 21 and 28 December 1964, L. Whitcomb (FSCA).

LOUISIANA; *Catahoula Par.,* Sicily Island (not town), 2M, 2F, 2 juvs., 12 October 1974, S. Ziser (FSCA).

In addition to these specimens, the record from Dallas County, Arkansas, locality not specified (Causey 1952b), is considered valid and is so indicated in figures 9 and 211. There is also an Arkansas sample in the FSCA containing two males, six females, and six juveniles from an unspecified location in Washington County. This site is so distant

from the others that I think it may represent a labelling error and prefer to omit it. For many years Dr. Causey's home was in Washington County, where she and others collected many eurymerodesmids. If *dubius* does occur there, I think it would have been collected more than once.

Since Causey's sketch of the gonopod of *Paresmus columbus* (1950a, fig. 11) closely resembles that of *dubius,* I include *P. columbus* in the synonymy and show its type locality, 3 miles east of Magnolia, Columbia County, Arkansas, as a literature record (Figs. 9, 211). The type series of *P. columbus* contained the male holotype and a female allotype, both of which are missing from the ANSP, the reported repository (Causey 1950a, Chamberlin and Hoffman 1958). No other localities have been recorded for *P. columbus.*

Remarks. — *Eurymerodesmus dubius* is one of the more flexible congeners, hence the large number of measurements since it was possible to uncoil many males without breakage. Like *goodi, dubius* may be confused with xystodesmids because of its large size. The relatively linear, upright telopodites are superficially similar to those of *digitatus* (compare figs. 47-48 and 199-200), a resemblance attributable to convergence. Likewise, their enclosure within the aperture is convergent with the condition in the *melacis* lineage.

The Louisiana locality is about 100 miles from the closest known site in Arkansas. Field work is therefore needed in northern Louisiana to determine whether these areas connect.

The **Varius** Group

The *varius* group is characterized as follows: apertures with divided lateral margins and caudolateral pouches; acropodites short, no more than 1/4 of the telopodite length, broadly terminal, and poorly demarcated from the prefemur at least in some populations of each component species; prefemora long, at least 3/4 of telopodite length, without distinct terminal lobes on outer surfaces in all populations. The subspecies of *varius* in southwestern Louisiana between the Pearl and Mississippi Rivers, *v. christianus,* possesses strong terminal prefemoral lobes that clearly demarcate the acropodite. However, this trait is not shared by all races of *varius.* The nominate subspecies, in the southeast along the Atlantic Coast, and some forms of *v. louisianae* in northern Louisiana lack distinct lobes, and the acropodite is therefore continuous with the prefemur. Other species have at most a slight lobe or swelling, so the key feature of the *varius* group is the absence of the lobe from some populations of each species. Since the *simplex* group contains forms with strong prefemoral shoulders and subterminal or narrowly terminal acropodites, *varius* itself bridges the anatomical gap between the two groups through its lobed forms. The two groups could therefore be combined, but it is convenient to segregate them based on the acropodal feature. The *varius* group covers nearly all of the range of the *Kewanius* lineage, extending from the Atlantic Ocean to eastern Texas, east-central Missouri, and southern Illinois, with an apparently allopatric population in Mason County, Texas (Figs. 213). The only regions that it does not encompass are the area occupied by *impurus,* Brazos and Washington counties, Texas, and west-central Missouri.

Components. — *varius* (McNeill) [*v. varius, v. christianus* Chamberlin, *v. louisianae* Chamberlin]; *newtonus* Chamberlin; *oliphantus* Chamberlin; *amplus* Causey; *elevatus,* new species.

Eurymerodesmus varius (McNeill)

Diagnosis. — A small to moderate-size species; males characterized by variable mandibular projection, ranging from minute, nubbinlike, and subequal to that of females to moderate-size; sides of aperture divided, with closed caudolateral pouches; telopodite long; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly to sharply demarcated from prefemur; latter with or without rounded distal lobe on outer margin, with relatively few hairs arranged sporadically and discontinously along inner surface; cyphopod valves of females with distal corners extending into angular ridge, angling toward corner; receptacle moderate-size, sides not curving around operculum.

Remarks. — The third oldest species in the family, *varius* occupies the largest distribution, covering the entire area east of the Mississippi River, with scattered, possibly relictual populations in north-central Louisiana and southern Arkansas (Fig. 54). The distal end of the gonopod prefemur undergoes an east-west clinal change ranging from either no, or only a slight, distal prefemoral swelling in populations along the Atlantic and Gulf Coast westward to western Alabama, to a somewhat larger swelling in those in Mississippi, to a strong, broadly rounded lobe in ones in southeastern Louisiana between the Pearl and Mississippi Rivers, to a variably small to moderate-size swelling in forms in northern Louisiana and Arkansas. As the swelling becomes larger,

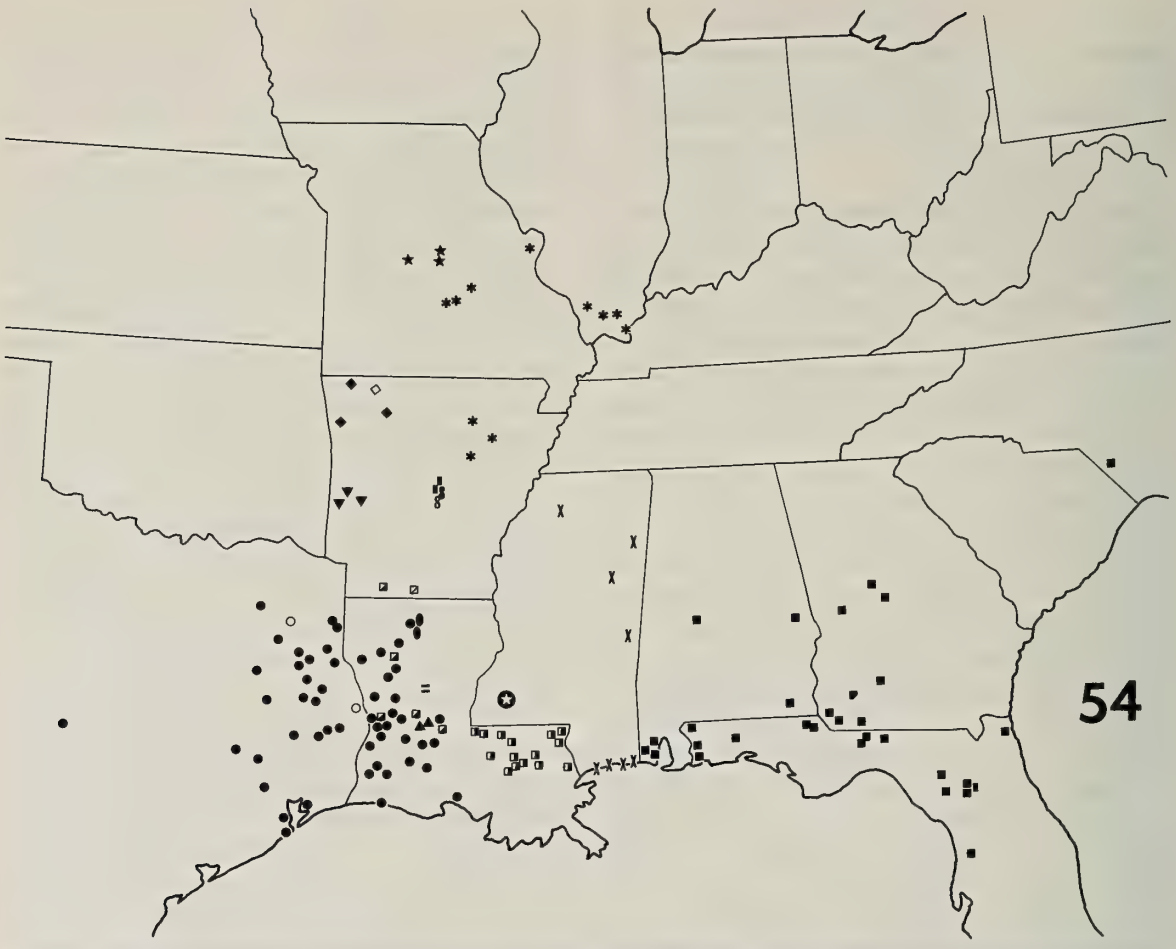


Fig. 54. Distributions of the *varius* and *simplex* groups. Squares, *varius varius;* X's, *varius* intergrades; vertical half-shaded squares, *varius christianus;* diagonal half-shaded squares, *varius louisianae;* dots, *amplus;* diamonds, *newtonus;* asterisks, *oliphantus;* stars, *elevatus;* upright triangles, *simplex;* inverted triangles, *polkensis;* star in dot, *caesariatus;* ovals, *paroicus;* equals sign, *crassatus;* 8's, *pulaski;* and rectangles, *serratus.* Open symbols denote literature records considered valid.

the acropodite becomes correspondingly more sharply demarcated, and in populations in southeastern Louisiana the latter is discontinuous with the prefemur, thereby resembling the condition in *simplex.* Most Atlantic populations exhibit a trace of a swelling, but a few lack this and have parallel-sided prefemora, such as that at the type locality, Pensacola, Escambia County, Florida. Accompanying these gonopodal changes is variation in the mandibular projection. All males from east of the Mississippi River display minute, rounded, and weakly sclerotized processes, at most only slight nubbinlike vestiges or rounded lobes subsimilar to those in females. The projection is larger and variable west of this boundary, being subtriangular and apically subacuminate in some males and still larger, more heavily sclerotized, and apically blunt or truncate in others. All forms possess sparsely and sporadically hirsute prefemora indicative of a single species, but the clinal changes in the distal prefemoral swelling and those involving the mandibular process are significant enough to justify taxonomic recognition at the subspecific level. Since the type locality is in the east, in the area occupied by forms with only slight swellings, they become the nominate subspecies, and *louisianae* Chamberlin was proposed for those in northern Louisiana and southern Arkansas with larger mandibular projections. No name is available for the lobed population in southeastern Louisiana, but *christianus* Chamberlin was proposed for an intergrade form with an intermediate swelling from Harrison County, Mississippi, only about 35 miles to the east. As first reviser, I conserve this name and assign it to the lobed population. At the Pearl River, the increase in size of the lobe is sharp and dramatic, but the change is more gradual to the east and appears to begin in Mississippi. Consequently, I consider the forms in this state as in-

KEY TO SUBSPECIES, BASED ON ADULT MALES

1. Projection of mandibular stipes weakly sclerotized, a rudimentary nubbin or short, rounded lobe, subsimilar to condition in females (Fig. 55) 2
   Projection larger, heavily sclerotized, subtriangular to blunt and truncate (Figs. 66-67) ..... *varius louisianae* Chamberlin
2. Gonopod prefemur with at most only a low, rounded distal swelling, only slightly elevated above outer surface; acropodite poorly demarcated (Figs. 57-58) ..... *varius varius* (McNeill)
   Prefemur with distinct terminal lobe, strongly elevated above outer margin; acropodite sharply demarcated (Fig. 65) ..... *varius christianus* Chamberlin

tergrades between *v. christianus* and the nominate subspecies, occurring from Alabama eastward. Triangular and blunt mandibular projections are intermixed in northern Louisiana and southern Arkansas, the area occupied by *v. louisianae.*

The clinal change in *varius* from parallel-sided to lobed individuals is significant because it links the continuous, broadly terminal, and poorly demarcated acropodal forms clearly assignable to *Eurymerodesmus* to the narrowly terminal, strongly demarcated, and discontinuous acropodite of *simplex,* type species of *Kewanius,* which in turn bridges the anatomical gap to the subterminal acropodal forms assignable to *Paresmus.* Consequently, this clinal change provides the necessary evidence to synonymize the last two genus-group names with *Eurymerodesmus. Eurymerodesmus varius* is thus an intermediate species connecting all these forms into a single assemblage, but for convenience and ease of comprehension, I divide it into two groups based on poorly or sharply demarcated acropodites. Since this structure is continuous in most populations, *varius* is the oldest available name for the poorly demarcated form and is therefore used to designate this species group.

There are several very large samples of the nominate subspecies, *v. christianus,* and some sizeable ones of intergrades, particularly those taken in pitfall traps. I could also have collected scores of individuals at the North Carolina, and Alachua and Gilchrist counties, Florida, sites. These numbers suggest that studies on population structure and ecology of *varius* would be fruitful.

Eurymerodesmus varius varius (McNeill), new status
Figs. 54-61

Polydesmus varius McNeill, 1887:323-324.
Leptodesmus varius: Bollman, 1888b:344.
Eurymerodesmus minimus Loomis, 1943;320, fig. 2.
Eurymerodesmus varius: Causey, 1954:67. Chamberlin and Hoffman, 1958:81.

Type specimen. — Female holotype (NMNH) collected by C. H. Bollman, March-April 1886, at Pensacola, Escambia Co., FL. The original description (McNeill 1887) indicates that the type series contained three females, but the other two are lost. Housed with the holotype is a vial labeled "*Leptodesmus varius* McNeill, type specimen," containing a male of this form supposedly collected at an unknown site in Indiana. The source of this specimen is unknown, but it is not part of the type series and represents a labeling error since no authentic Indiana localities are known for a eurymerodesmid. It is ignored in this study.

Diagnosis. — A small subspecies; males with projection of mandibular stipes minute, nubbinlike, indistinct; acropodite essentially smoothly continuous with, and poorly demarcated from, prefemur; latter with at most only a slight suggestion of distal swelling, weakly elevated above margin.

Color in life. — Peritremata pink; metaterga mottled brownish olive with narrow pink stripes along caudal edges connecting peritrematal markings; collum with pink stripes along both anterior and posterior margins. Loomis (1943) described the living color as "translucent white with a light pinkish tinge," which fades rapidly in alcohol.

Male topotype. — Length about 14.2 mm, maximum width 1.8 mm, W/L ratio 12.7%.

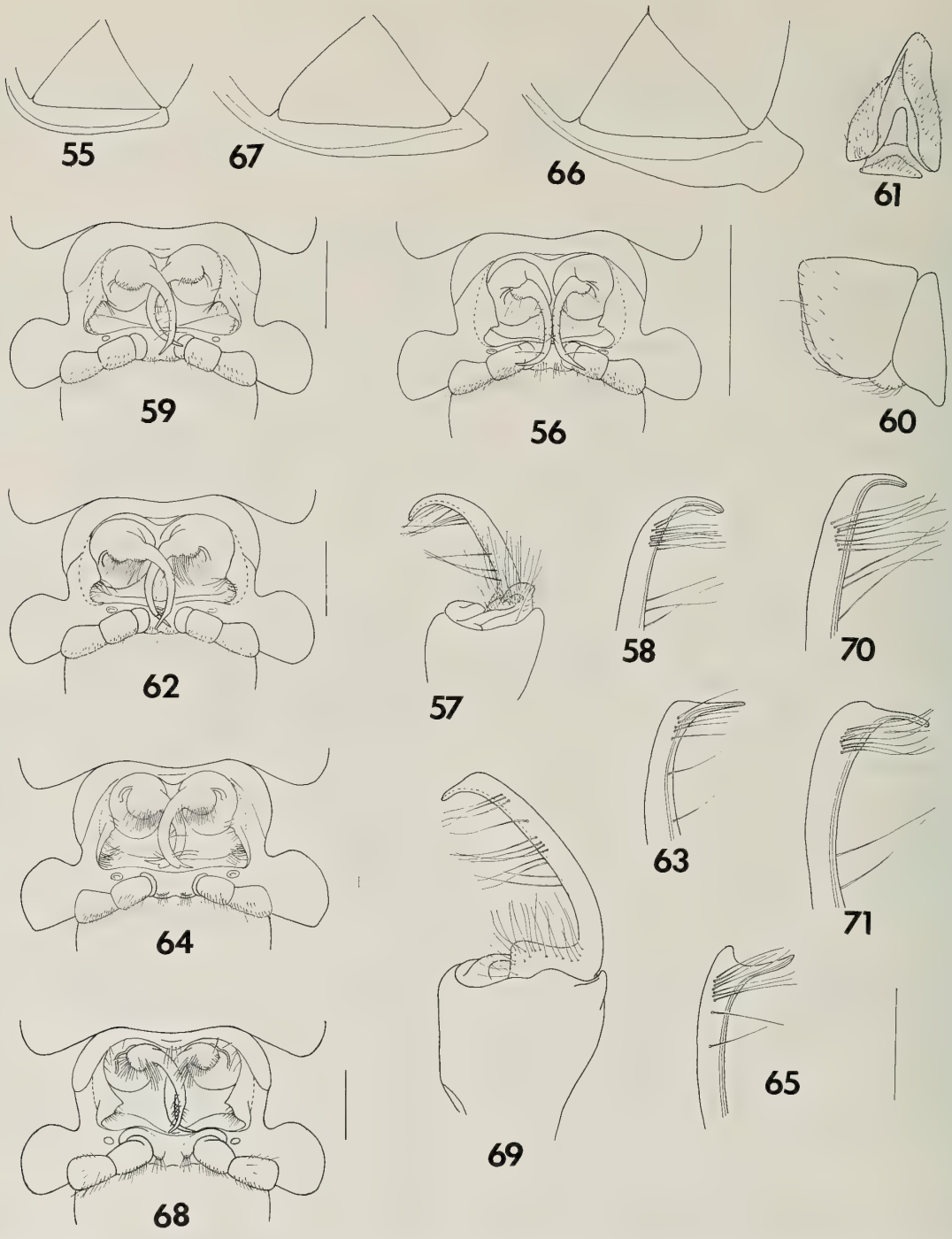
Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 1.3 mm, interantennal isthmus 0.4 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres $2>3>4=5=6>1>7$. Genae without impressions. Facial setae as follows: epicranial and subantennal absent, interantennal 1-1, frontal 1-1, genal 3-3, clypeal about 10-10, labral about 14-14. Mandibular stipes with minute, vestigal projection, corner rounded, of general size and configuration as that of female eurymerodesmids, subsimilar to females of *varius* (Fig. 55).

Collum extending slightly below ends of following tergite. paranota depressed, continuing slope of dorsum; posterior corners rounded through segment 7, blunt on 8-13, becoming progressively more acute caudad.

5th and 6th sterna without elevations, with moderate hair patches adjacent to leg coxae. Postgonopodal sterna with minute hirsute lobes between 9th legs, remaining sterna flat and unmodified, with faint transverse grooves and sparse hair patches disappearing in midbody region, caudal sterna glabrous. 2nd coxae without projections. Prefemoral lobes relatively small, restricted to pregonopodal legs.

Gonopodal aperture (Fig. 56) broadly rectangular, with variable caudolateral pouches, slightly indented anteriad at midline, 1.0



Figs. 55-71. *Eurymerodesmus varius*. 55-61, *varius varius*. 55, projection of right mandible of topotype, lateral view. 56, aperture and gonopods *in situ* of topotype, ventral view. 57, left gonopod of the same, lateral view. 58, telopodite of the same, medial view. 59, aperture and gonopods *in situ* of male from Robeson Co., NC, ventral view. 60, left cyphopod of holotype, caudal view. 61, the same, medial view. 62-63, *varius* intergrades. 62, aperture and gonopods *in situ* of male from Harrison Co., MS, ventral view. 63, telopodite of left gonopod of the same, medial view. 64-65, *varius christianus*. 64, aperture and gonopods *in situ* of male from Washington Par., LA, ventral view. 65, telopodite of left gonopod of male from Ascension Par., LA, medial view. 66-71, *varius louisianae*. 66, right mandibular process of holotype, lateral view. 67, right mandibular process of paratype, lateral view. 68, aperture and gonopods *in situ* of holotype, ventral view. 69, left gonopod of the same, lateral view. 70, telopodite of the same, medial view. 71, telopodite of left gonopod of male from Columbia Co., AR, medial view. Scale lines for figs. 56, 59, 62, 64, and 68 = 1.00 mm. Line for other figs. = 0.40 mm for 55, 66-67, and 69; 0.50 mm for 57-58, 60-61, 63, 65, and 70-71.

mm wide and 0.5 mm long at maxima, outline of apparatus slightly trapezoidal; anterior indentation minute, broadly rounded, barely perceptible; sides angling progressively mediad, leaning over aperture, and becoming progressively more elevated to division point located caudad over caudal margins, inner lateral margin plunging into opening and curving into inner caudal margin, obscured by lean of flare and outer lateral margin, latter leaning strongly mediad but angling laterad and dropping to metazonal surface at caudolateral corner, forming closed pouch with inner margin, rims essentially smooth; inner caudolateral corner smoothly curved, obscured by lean of flare; outer caudolateral corner rounded; inner caudal margin curving gently and bisinuately, subparallel to outer caudal margin; latter flush with metazonal surface, angling slightly caudad in midline; margins glabrous except for slight hair tufts in cavity. Gonopods *in situ* (Fig. 56) with telopodites curving mediad, touching opposite member in midline, then curving broadly laterad, extending well beyond aperture and terminating over coxae or prefemora of 9th legs. Gonopod structure as follows (Figs. 57-58): Telopodite relatively long, terminating at about level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, sides parallel for most of length, narrowing slightly and curving distad, with only 3-4 widely separated hairs on inner margin of proximal part of stem and distomedial tuft of 9 moderately separated hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from, prefemur, continuing broad dorsolateral curvature of latter, narrowing rapidly to subacuminate tip.

Female Holotype. — Body fragmented, length unmeasurable (15 mm according to McNeill (1887)), maximum width 1.7 mm, W/L ratio 11.3%. Agreeing closely with male topotype in somatic features, with following exceptions: Genal setae 1-1. Segments 3-8 with moderate elevations lateral to legs, highest on segments 3-4. Sterna glabrous, flat and unmodified, with incomplete transverse impressions originating between leg coxae.

Cyphopodal aperture elliptical, sides strongly elevated above metazonal surface. Cyphopods *in situ* with distal edges of valves visible in aperture, open side facing dorsad. Valves (Figs. 60-61) relatively large, subequal, completely filling respective sides of aperture, moderately hirsute, distal corners extending ventrad into distinct ridge, bluntly angular at corners. Receptacle moderate in size, glabrous, located laterad to valves, corners not extending partly around operculum, hidden internally under side of aperture. Operculum minute, located under open, dorsal side of valves.

Variation. — The Escambia County males agree closely with each other, the only exception being slight differences in the slope of the flare, or outer lateral margin, of the aperture. When the angle of slope is greater, the aperture extends farther laterad and the caudal edge is folded, as shown by a North Carolina male (Fig. 59). The slope of the flare also affects the size and shape of the pouch, and the degree to which it is open or closed; the cavity is narrower and more closed in males with more gradual slopes. The corner of the division point, the highest point on the sides, extends inward and downward or dorsad in males throughout the range.

The gonopods vary in the distance they project caudad, which is a measure of how tightly the body is coiled. Normally, they overhang the sternum between the 9th legs or the adjacent coxae, but occasionally they extend over more of segment 8. In more tightly coiled specimens, the 6th metazonite may extend over as much as half of the aperture. Topotypical males from Escambia County lack any trace of a distal prefemoral swelling, but most individuals from Georgia, Florida, North Carolina, and Alabama display a suggestion of an enlargement.

Ecology. — Causey (1954) collected this subspecies under live oaks in Escambia County, Florida. Habitat notations on vial labels include the following: in house on floor (Alachua Co., FL), under logs (Grady Co., GA), in roadside stream (Okaloosa Co., FL), in pine hardwood litter (Monroe Co., GA), and under horse dung (Gilchrist Co., FL). The samples from Tall Timbers Research Station, Leon County, and Big Bend Horticultural Lab, Jefferson County, Florida, were recovered from pitfall traps, and in at least one sample from the latter site, the trap was under a pecan tree.

In North Carolina, *v. varius* is plentiful at a rural residence in Robeson County, the only known site of eurymerodesmids in the state. They occur under pine and oak logs and in pine litter under azaleas and sesanqua bushes. I thought that this population might be introduced, but the family has resided there for over 20 years, and the shrubs were present when they came. Consequently, this seems a natural population, suggesting that *v. varius* will eventually be found at other sites in southeastern North Carolina and also in coastal South Carolina, where it has not been encountered. This population probably is not the source of the *Eurymerodesmus* sp. or "*Leptodesmus hispidipes*" records from Duke Forest, Durham County (Brimley 1938, Causey 1940, Wray 1967), which I (1978) deleted from the North Carolina fauna, since Causey's illustration (1940, fig. 8) is of a species with continuous prefemoral hairs. Thus, *Eurymerodesmus* is still unknown from piedmont North Carolina. I have searched for it repeatedly in Duke Forest and neighboring areas at appropriate times of the year without success.

In Florida, *v. varius* inhabits a variety of biotopes. In Gilchrist County I found a sizeable population in and under exposed, rotting oak logs and stumps on sandy substrate. Large populations were also encountered in hardwood litter at Fort Caroline, Duval County, and Marjorie Kinnan Rawlings State Historic Site, Alachua County. The latter site is a mesic hardwood hammock dominated by sweet gum, laurel oak, and cabbage palm without pine.

The Hernando County locality also is a hardwood forest, but it contains more oak trees and is more xeric.

Distribution. — The Atlantic and Gulf Coastal Plains of the southeastern United States, from southeastern North Carolina to Hernando County, Florida, and inland to the Fall Zone Region of Alabama and Georgia as far west as Mississippi (Fig. 54). I investigated many sites in peninsular Florida in January 1988 to determine the southern range limit for the species and family along the Atlantic Coast and did not find it east of the St. John's River. Consequently, Ft. Caroline, less than 10 miles from the ocean, is the only known locality in eastern Florida. On the western side of the peninsula I extended the range southward about 80 miles, from Gainesville to northern Hernando County, but did not encounter the milliped farther south, even in hardwood areas around Brooksville where *Sigmoria (Cheiropus) planca* (Loomis) occurs (Shelley 1984b). These hardwood communities end in Hernando County, and the habitat around Tampa Bay and farther south is unsuitable. Consequently, northern Hernando County seems to be near the actual southern range limit for both *v. varius* and the Eurymerodesmidae along the Atlantic Coast. No records are available from South Carolina, but the milliped should be expected throughout the southeastern Coastal Plain judging by its occurrence in North Carolina and the general uniformity of coastal environments in the Carolinas and Georgia. I doubt if this is an allopatric locality, as occur in *hispidipes* and *serratus,* and the absence of South Carolina records probably reflects the absence of winter collecting. Specimens were examined as follows:

NORTH CAROLINA: *Robeson Co.,* 1.2 mi. SW Proctorville, along SR 2265, 0.4 mi. W jct. NC hwy. 130, M, 17 April 1984, D. Hedgepeth (NCSM); 28M, 20F, 17 April 1985, R. M. Shelley and J. Alderman (NCSM); and 6M, 9F, 4 November 1986, R. M. Shelley (NCSM).

GEORGIA: *Monroe Co.,* 5 mi. N Lizella, 2M, F, 19 February 1983, J. A. Payne (RLH). *Bibb Co.,* Macon, juv. M, date unknown, L. M. Underwood (NMNH). *Talbot Co.,* Geneva, 2F, 24 April 1960. L. Hubricht (RLH). *Baker Co.,* near Newton, Pineland Plantation, 5M, 4F, 30 March 1959, D. B. Jester, H. Wyatt (FSCA). *Worth Co.,* 4 mi. E Sylvester, 6F, 6 juvs., 11 June 1959, N. B. Causey (FSCA). *Seminole Co.,* 4 mi. NW Donaldson, 4M, 3F, 18 March 1961, L. Hubricht (RLH). *Decatur Co.,* near Spring Cr. W of Brinson, 2M, F, 18 March 1961, L. Hubricht (RLH). *Grady Co.,* 3 mi. W Cairo, 3M, 3F, 26 January 1965, N. B. Causey (FSCA).

FLORIDA: *Duval Co.,* Ft. Carolina, 6M, 7F, 8 November 1985, R. M. Shelley (NCSM). *Alachua Co.,* Gainesville, F, 29 October 1959, W. J. Platt (FSCA); and Marjorie K. Rawlings St. Hist. Site, 31M, 22F, 21 January 1988, R. M. Shelley and G. B. Edwards (NCSM). *Gilchrist Co.,* S. of Trenton, 6 juvs., 2 April 1959, R. E. Woodruff (FSCA); and along FL hwy. 340 at Suwannee R., 19M, 14F, 6 November 1985, R. M. Shelley (NCSM). *Hernando Co.,* 7 mi. NNE Brooksville, along US hwy. 40, 2M, 3F, 22 January 1988, R. M. Shelley (NCSM). *Leon Co.,* Tall Timbers Res. Sta., 34M, 22F, 23 April 1969-24 January 1972, P. Fall, W. W. Baker, and W. H. Whitcomb (FSCA); and Tallahassee, F, 10 November 1958, R. McFarland (FSCA). *Jefferson Co.,* locality and collector unknown, 47M, 31F, 20 November 1968 - 7 February 1969 (FSCA); and Big Bend Hort. Lab near Monticello, 52M, 32F, 2 February 1969 - 12 December 1969, W. H. Whitcomb (FSCA). *Jackson Co.,* Marianna, F, 6 June 1970, D. C. Bennett (FSCA), M, date and collector unknown (MCZ), and juv., 27 October 1941, E. M. Loomis (NMNH); and Florida Caverns St. Pk., 19 juvs., 27 May 1958 - 2 July 1960, N. B. Causey (FSCA). *Okaloosa Co.,* locality unknown, 5M, 10F, 14 March 1961, H. A. Denmark (FSCA). *Escambia Co.,* Pensacola, F, March-April 1986, C. H. Bollman (NMNH), and 3M, 5F, 15 March 1970, C. Seal (FSCA) TYPE LOCALITY; Cantonment, 5M, F, 1 May 1954, N. B. Causey (FSCA); and 5 mi. S Atmore, AL, F, 27 November 1964, E. Harvey (FSCA).

ALABAMA: *Perry Co.,* 6 mi. NW Marion, 3F, 6 January 1954, N. B. Causey (FSCA). *Lee Co.,* Auburn, M, 4F, date unknown, B. B. Warwick (NMNH), 2M, 2F, 1898, F. Farley (NMNH), and M, 6F, 3 juvs., 13 June 1959, N. B. Causey (FSCA). *Houston Co.,* "Brannon Stand" along US hwy. 84, 2M, 3F, 10 juvs., 26 January 1954, N. B. Causey (FSCA). *Mobile Co.,* "Seven Hills," 5M, 2F, 6 April 1958, S. Lazell (FSCA); Bellingrath Gardens, M, 22 January 1965, N. B. Causey (FSCA); and roadside park along US 90 E of Pascagoula, MS, 3F, 21 January 1965 (FSCA).

Eurymerodesmus varius christianus Chamberlin, new status
Figs. 54, 64-65, 211

Eurymerodesmus christianus Chamberlin, 1946:140, fig. 5. Chamberlin and Hoffman, 1958:79. Causey, 1963:77-78.

Type specimens. — Male holotype, female allotype, and two male paratypes (NMNH) collected by J. and W. Rapp, 16 February 1946, at Pass Christian, Harrison Co., MS. As stated in the species account, these specimens actually belong to intergrade populations, but since no name is available for the lobed form in eastern Louisiana and this site is only about 35 miles to the east, it is appropriate to conserve *christianus* and assign it to this race.

Diagnosis. — A small subspecies; males with projection of mandibular stipes minute, nubbinlike, indistinct; acropodite discontinuous with, and sharply demarcated from prefemur; latter with high, rounded distal lobe, strongly elevated above distal margin (Figs. 64-65).

Variation. — In some males, the corner of the division point of the aperture extends downward well into the opening, nearly touching the gonopodal coxae, and in specimens from East Baton Rouge Parish, the outer caudal margin is rimmed and extends into the opening. On the gonopods the prefemoral lobe in some males leans dorsad rather than being aligned with the stem.

Ecology. — Specimens from East Baton Rouge Parish were collected in magnolia woods and under dead leaves and grass around a house foundation.

Distribution. — Southeastern Louisiana between the Pearl and Mississippi Rivers (Figs. 54, 211). Specimens were examined as follows:

LOUISIANA: *Washington Par.,* Angie, 2M, 2F, 2 May 1958, J. L. Crain (FSCA) and 68M, 79F, 12 December 1958, collector unknown (FSCA); 7 mi. S Angie, 10M, 4F, 16 and 24 November 1958, J. L. Crain (FSCA); and 6 mi. SW Bogalusa, 2F, 21 January 1965, N. B. Causey (FSCA). *St. Tammany Par.,* 5 mi N Hickory, F, 21 February 1965, W. Longest (FSCA); and 1 mi. E Covington, 2 juvs., 2 December 1980, M. R. and J. E. Cooper (NCSM). *Tangipahoa Par.,* 1 mi. N Hammond, F. 23 December 1964, R. E. Randy (FSCA); and 6 mi. E Ponchatula, 24 March 1962, K. A. Arnold (FSCA). *St. Helena Par.,* Grangeville, M, 11 December 1963, S. Geauthreaux (FSCA). *Livingston Par.,* 2.8 mi. W Killian, F, 2 May 1971, D. A. Rossman (FSCA). *East Feliciana Par.,* nr. S gate LA state prison, 3M, 3F, 1970, collector unknown (FSCA). *Ascension Par.,* nr. Prairieville, 6M, 3F, 20 January 1965, W. Longest (FSCA). *East Baton Rouge Par.,* locality unknown, 2M, 5F, 4 November 1959, collector unknown (NMNH) and 3M, 3F, 7 November 1964, collector unknown (FSCA); Baton Rouge, 2M, 3F, November 1969, and M, 2F, 25 October 1964, collectors unknown (FSCA), 2M, F, 11 November 1963, W. J. Harman (FSCA), and M, F, 2 juvs., 9 January 1971, D. A. and C. E. Rossman (FSCA); LSU and environs, 3M, 2 February 1964, and M, F, 9 juvs., 12 December 1964, R. E. Tandy (FSCA); and LSU farm, M, 20 February 1963, B. Hepburn (FSCA).

Eurymerodesmus varius louisianae Chamberlin, new status
Figs. 54, 66-71, 211

Eurymerodesmus louisianae Chamberlin, 1942a:6, pl. 2, fig. 17. Chamberlin and Hoffman, 1958:80.

Eurymerodesmus spectabilis Causey, 1950a:270, figs. 6-7; 1952b:2. Chamberlin and Hoffman, 1958:81. **NEW SYNONYMY.**

Type specimens. — Male holotype and one male paratype (NMNH) collected by L. Hubricht, 12 April 1936, 2 mi. S Saline, Natchitoches Par., LA. The original description (Chamberlin 1942a) stated that the type series contained a male and female, labeled allotype in the vial, an example of sex misdetermination.

Diagnosis. — A small to moderate-size subspecies; males with projection of mandibular stipes distinct, moderately long, triangular to blunt (Figs. 66-67); acropodite poorly to moderately demarcated from prefemur; latter with variable distal swelling weakly to moderately elevated above distal margin (Figs. 69-71).

Color in Life. — Paranota red; metaterga dark brown with red stripes along caudal margins, probably connecting with paranotal markings (Chamberlin 1942a). Causey (1950a) confirmed the striped pattern, reporting orange rather than red and stripes along both margins of the collum. She noted further that the metatergal stripe is interrupted on some caudal segments, that the stripe is replaced by four orange dots in some specimens, and that the orange pigment was so intense in some individuals that they appeared entirely orange from a distance.

Variation. — The holotype has an oblong, blunt mandibular process (Fig. 66), but it is triangular (Fig. 67) in the paratype, presumably collected at the same place and time. Both conditions are also displayed by males in Avoyelles and Catahoula parishes. The Arkansas male and those from Rapides and Avoyelles parishes have moderate distal swellings on the gonopod prefemora (Fig. 71), resulting in a slightly discontinuous, moderately demarcated acropodite. The telopodites of individuals from Natachitoches and Rapides parishes curve more dorsad than laterad, best seen *in situ*

(Fig. 68). Thus, they resemble the condition in *amplus,* but they lack continuous hairs on the prefemoral stem. Some males of this race have more prefemoral hairs than do those of the other subspecies, but the hairs are not continuous or regularly spaced. Thus, the main distinctions between *amplus* and *v. louisianae* are the regularity of hairs on the prefemoral stem combined with the *in situ* orientation of the gonopods.

Ecology. — According to Causey (1950a), the Arkansas specimens were taken in a climax pine-hardwood area. The label with the type specimens states that they were encountered under logs; that with the Rapides Parish specimens indicates that they were found under cow dung.

Distribution. — Known from six scattered localities from southern Arkansas to central Louisiana (Figs. 54, 211). Specimens were examined as follows:

ARKANSAS: *Columbia Co.,* Magnolia, M, F, 24 December 1949, N. B. Causey (ANSP).

LOUISIANA: *Natchitoches Par.,* 2 mi. S Saline (in Bienville Par.), 2M, 12 April 1936, L. Hubricht (NMNH) TYPE LOCALITY. *Vernon Par.,* 2.7 mi. NE Caney, M, 8 April 1967, L. D. Wilson (FSCA). *Avoyelles Par.,* Evergreen, M, 28 October 1965, M. Kordish (FSCA). *Rapides Par.,* Forest Hill, 2M, F, 11 December 1945, R. Wenzel (FMNH). *Catahoula Par.,* 1 mi. WNW Harrisonburg, 2M, F, 25 April 1971, D. A. Rossman (FSCA).

Remarks. — Causey (1963) recorded this form from an unspecified locality in Union County, Arkansas. The specimens were supposedly in her collection, but they are not among the material now at the FSCA.

With only six scattered samples from an area that has been reasonably well collected, *v. louisianae* may be a relictual form, declining naturally toward extinction. The most obvious cause would be swamping by *amplus,* which is widespread and abundant in Louisiana west of the Mississippi River. However, much more field work is necessary in this area to search for *v. louisianae* as well as components of the *simplex* group.

Shelley and Whitehead (1986) defined subspecies in *Sigmoria* as reasonably homogeneous taxa that connect with other such taxa through intergrades. Populations had to be continuous for subspecies to be applicable; when there were hiatuses, the species category was employed even if intermediates were known. Populations of *varius* are continuous up to the Mississippi River, then there is a gap of about 40 miles to the closest known site of *v. louisianae,* in Avoyelles Parish. I therefore debated for some time the status of this race before reasoning that the similarities between the gonopods of *v. louisianae* and those of the other races is so close that specific status based solely on the mandibular projection was unreasonable. This decision should be reviewed by future workers with access to more material and particularly ones who can sample between West Feliciana and Avoyelles parishes, to try to connect *v. louisianae* and *v. christianus.*

Aside from fewer prefemoral hairs, the differences between *v. louisianae* and *amplus* are subtle. They differ in size, with *v. louisianae* being small while *amplus,* though variable, is larger. The apertures of *v. louisianae* and the form of *amplus* in northern Louisiana are closely similar, but there are gonopodal distinctions. Best seen *in situ,* the acropodites bend more strongly from the prefemur and are directed more laterad in *v. louisianae,* whereas in *amplus* they are curved and extend in a dorsal direction thus being more continuous with the axis of the prefemur. Finally, the prefemur of *v. louisianae* often exhibits a slight but distinct distal swelling on the outer surface, whereas there is no trace of this feature in *amplus.* The combination of this swelling and the sparsely hirsute condition resembles that in *v. christianus.* Causey (1963) provides a clue to the status of *v. louisianae* by placing the synonym *spectabilis* under *christianus,* indicating that she too was influenced by the prefemoral similarities, particularly the sparse hairs.

The similarities between *v. louisianae* and *amplus* pose a difficult taxonomic problem. Since some males of the former have more prefemoral hairs than occur on other subspecies, they could be regarded as intergrades between the sparsely and sporadically hirsute stems and those with dense, continuous hairs. Furthermore, the acropodites of some males of *v. louisianae* are more aligned with the prefemur and curve dorsad *in situ* rather than laterad, a condition that could also be interpreted as intermediate between *varius* and *amplus.* Thus, the question arises as to whether *amplus* and *varius* are indeed reproductively isolated, and the argument that they should be combined carries considerable merit. Others analyzing the available material might consider some of my samples of *v. louisianae* to be *amplus.* For clarity, I separate these forms and describe the situation. The complexity in a single species combining the multitude of forms of *varius* and *amplus* is more than I can handle on first revision, and additional material may always clarify the picture. Final resolution is therefore left to future

workers, particularly persons in Louisiana who can meticulously sample its eurymerodesmid fauna.

Eurymerodesmus varius intergrades
Figs. 54, 62-63

I combine under this heading forms with moderate distal prefemoral swellings (Figs. 62-63), intermediate between the strong lobes of *v. christianus* and the slight enlargements of the nominate subspecies. As stated in the species account, the enlargements become more noticeable in Mississippi, and the boundary of the strongly lobed race is sharp, the Pearl River. Thus, I consider all records of *varius* from Mississippi as intergrades.

Ecology. — The following habitat notes are on vial labels: under strawberries in strawberry field, and under boards and rocks, Jackson Co.; "waste ground," Lauderdale Co.; and in pitfall traps in cotton field, Oktibbeha Co.

Distribution. — Mississippi (Fig. 54). Specimens were examined as follows:

MISSISSIPPI: *Panola Co.,* 13 mi. E Como, 5M, 3F, 25 December 1964, W. Longest (FSCA). *Monroe Co.,* Aberdeen, 3M, 3F, 6 March 1961, R. E. Hutchins (FSCA). *Oktibbeha Co.,* Craig Springs, 10 mi. S Starkville, 18M, 23F, jv., 1 October - 31 December 1979, W. H. Cross (MEM, NCSM). *Newton Co.,* Decatur, many juvs., 5 May 1933, H. Janes (NMNH). *Lauderdale Co.,* Meridian, 1st St. and 53rd Ave., 5M, 6F, 10 December 1961, L. Hubricht (RLH). *Stone Co.,* MS hwy. 15 at Harrison Co. line, 2F, date unknown, N. B. Causey (FSCA). *Jackson Co.,* Pascagoula, 2M, 3F, 12 February 1962, T. Sheldon (FSCA); Spanish Fort, 10M, 4F, 21 January 1965, N. B. Causey (FSCA); 3 mi. N Fontanbleau, 11M, 12F, 1 January 1954, N. B. Causey (FSCA); and Gulf Coast Res. Lab, Ocean Springs, 3M, 7F, 27 November 1964, C. Guise (FSCA). *Harrison Co.,* Biloxi, 20 juvs., 12 July 1927, H.A. Robinson (NMNH). Gulfport, M, 2F, 18 November 1922, E. K. Bynum (NMNH); and Pass Christian, 2M, 2F, 16 February 1945, J. and W. Rapp (NMNH).

Remarks. — The type collection of *christianus* contains a gonopod of *angularis* that appears to have been accidentally placed in the wrong vial, probably by Causey when she was examining and comparing eurymerodesmids years ago. A gonopod of the holotype of *wellesleybentoni,* a synonym of *angularis,* is missing, and the extraneous gonopod in the *christianus* vial conforms closely to the remaining one in the *wellesleybentoni* vial.

Eurymerodesmus amplus Causey
Figs. 54, 72-82, 211-212

Leptodesmus hispidipes: Brolemann, 1895:67. Chamberlin, 1918:370 (in part).

Fontaria (Eurymerodesmus) hispidipes: Brolemann, 1900:129, fig. 32.

Eurymerodesmus amplus Causey, 1952b:4, fig. 3. Chamberlin and Hoffman, 1958:78.

Eurymerodesmus hamatilis Loomis, 1969:250-251, figs. 11-13. **NEW SYNONYMY.**

Eurymerodesmus hispidipes: Stewart, 1969:384.

Type specimens. — Male holotype and female allotype (AMNH) collected by W. J. Harmon in November 1951 at Ruston, Lincoln Par., LA.

Diagnosis. — A moderate-size species; males characterized by long mandibular projections; sides of aperture divided, with variably closed to partly open pouch; telopodite long; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners extending into distinct ridge of variable length and configuration, sublinear or angling toward corner, with or without terminal papilla in more angular forms; receptacle moderate-size, sides curving partly around operculum.

Color in Life. — Paranota red; metaterga dark speckled olive with red stripes along caudal margins connecting paranotal spots, stripes partly obliterated by intrusions of base color; collum with red stripe along anterior margin.

Holotype. — Body highly fragmented, length unmeasurable, maximum width 4.2 mm.

Somatic features similar to *hispidipes,* with following exceptions:

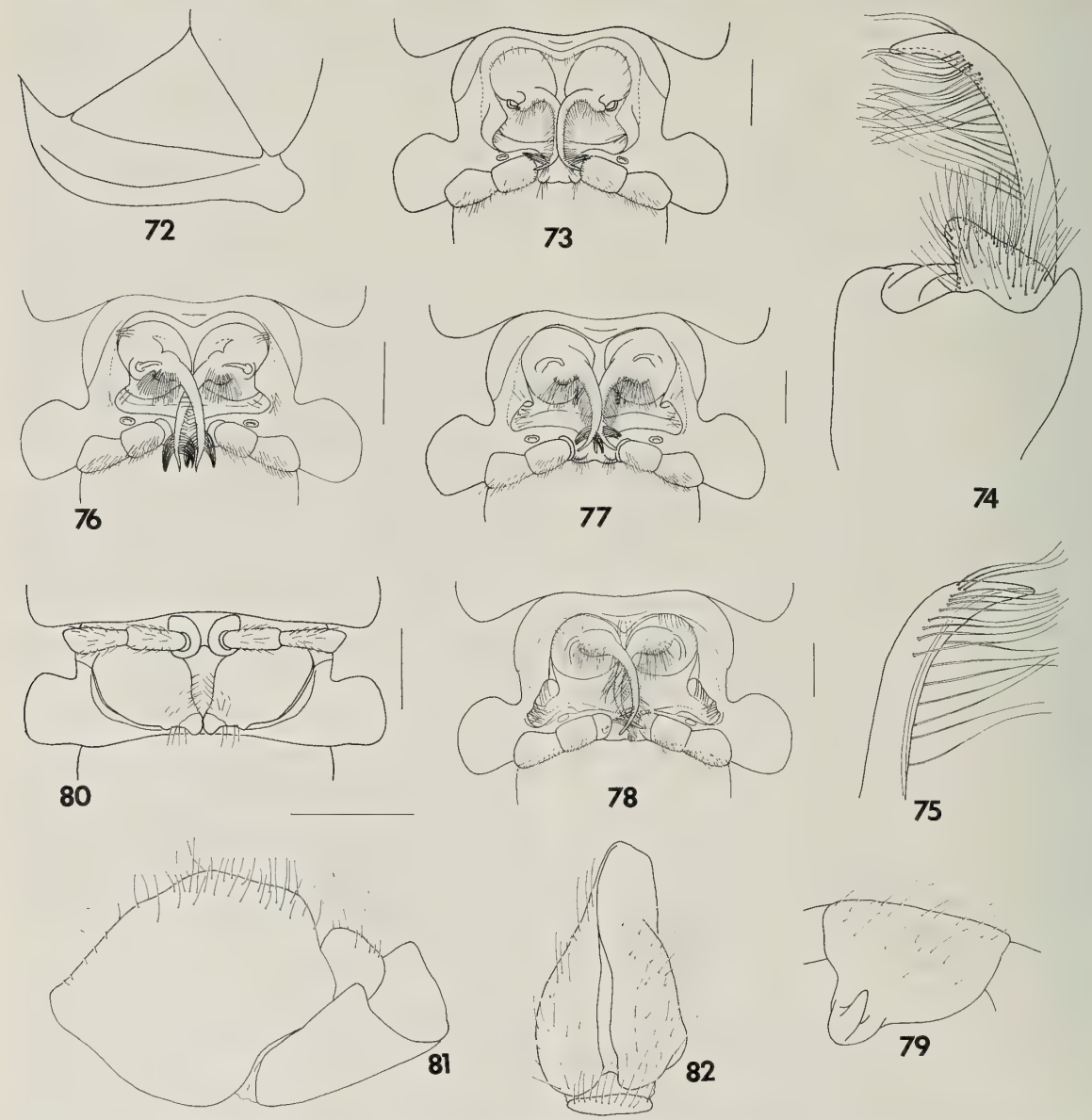
Width across genal apices 3.0 mm, interantennal isthmus 0.7 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and genal absent, subantennal 1-1, frontal 1-1, clypeal about 16-16, labral about 22-22. Process of mandibular stipes moderately long, broadly rounded apically, curving slightly inward at midlength (Fig. 72).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 9, blunt on 10-12, becoming progressively more acute caudally.

5th and 6th sterna with widely separated knobs between leg pairs. Postgonopodal sterna with narrowly segregated, elevated patches between 9th legs; remaining sterna becoming progressively flatter and less hirsute caudally. 2nd coxa with large, subconical anterior, and smaller rounded posterior lobes. Prefemora with broad lobes on outer surfaces of legs through segment 11.

Gonopodal aperture (Fig. 73, not this specimen) broadly ovoid, with closed, caudolateral pouches and moderate anterior indenta-

tion, 1.6 mm wide and 1.0 mm long at maxima, outline of entire apparatus irregularly hexagonal; anterior indentation short, apically rounded; sides divided, curving broadly mediad, leaning over opening, elevating gradually to division point near midlength, inner lateral margin curving dorsolaterad then blending smoothly into inner caudal margin, outer lateral margin leaning over opening, angling moderately laterad then curling mediad to metazonal surface at caudolateral corner, forming closed pouch with inner margin, rims slightly irregular; inner caudolateral corner smoothly curved but hidden by overhanging outer lateral margin; outer caudolateral corner moderately sharp, forming approximately a 60° angle; inner caudal margin extending linearly across midline, not parallel with outer caudal margin; latter curving along anterior surface of coxal condyles, extending caudad in midline; margins irregularly hirsute, with long hairs arising sporadically from anterior rim and overhanging opening, particularly along indentation and anterolateral corners, with additional short hairs arising from outer surface of outer lateral margin and moderate tufts from pouches. Gonopods *in situ* (Fig. 73, not this specimen) with telopodites lying partly over and under one another in midline of aperture, diverging at level of caudal margins, curving gently subdorsad and terminating over 9th coxae. Gonopod structure as follows (Figs. 74-75): Telopodite terminating well before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite



Figs. 72-82. *Eurymerodesmus amplus*. 72, projection of right mandible of holotype, lateral view. 73, aperture and gonopods *in situ* of topotype, ventral view. 74, left gonopod of holotype, lateral view. 75, telopodite of the same, medial view. 76-78, aperture and gonopods *in situ* of males from Evangeline and Calcasieu pars., LA, and Angelina Co., TX, respectively, ventral views. 79, prefemur of left 7th leg of male from Angelina Co., anterior view. 80, cyphopods *in situ* of female from Vernon Par., LA, ventral view. 81, left cyphopod of allotype, ventral view. 82, the same, medial view. Scale lines for figs. 73, 76-78, and 80 = 1.00 mm. Line for other figs. = 0.30 mm for 72 and 79, 0.40 mm for 74 and 81-82, and 0.50 mm for 75.

length, stem leaning over coxa for most of length, more so distad, sides parallel throughout, with two rows of continuous, regularly spaced hairs along inner margin, angling slightly outward distad, and distomedial tuft of about 10 hairs. Acropodite short and broadly terminal, only about 1/8 of telopodite length, continuing curvature of prefemur and directed dorsolaterad, smoothly continuous with, and poorly demarcated from prefemur, sides narrowing continuously to acuminate tip.

Allotype. — Length 30.7 mm, maximum width 4.2 mm, W/L ratio 13.7%. Agreeing closely with holotype in somatic features, with following exceptions: Process of mandibular stipes relatively large, extending distinctly from base, broadly triangular. Sterna with variably broad impressions in midline, with sparse hair tufts subtending coxae except on segments 17-18.

Cyphopodal aperture broadly rectangular, sides strongly elevated above metazonal surface. Cyphopods *in situ* with corners of valves protruding through opening, valves oriented transversely. Valves (Figs. 81-82) large, subequal, ventral margin elevated into rim, angling slightly distad and slightly longer at corner, medial margin moderately hirsute. Receptacle moderately large, glabrous, located laterad at bases of valves, sides curving partly around operculum. Latter small, hidden under free (anterior) side of valves.

Variation. — The colors reported above were of the specimens I collected in Harris County, Texas. According to Causey (1952b), the paranota of the types were reddish orange; she provided no additional color details. The label accompanying the specimens from Sulphur, Calcasieu Parish, Louisiana, states "orange," presumably referring to the paranota, so the color of this species may vary.

Eurymerodesmus amplus is difficult to comprehend on its own merits, not to mention the close similarities with *v. louisianae*. The gonopods exhibit little intraspecific variation, but there are three main aperture variants that tend to occupy different sectors of the range thus suggesting that subspecies may be warranted. However, there are enough instances where one variant also occurs in another sector or there are additional sympatric forms, that this possibility is obviated. Moreover, the anatomical diversity is greater in Texas, and one or more heterogeneous races there would conflict with comparatively homogeneous ones in Louisiana. Finally, female variation is not parallel and would therefore counter subspecies based on males. By not showing comparable differences at fairly sharp male boundaries, females also contraindicate specific statuses for the principle male variants. Females show a general clinal trend toward a longer and more angular valvular ridge in a southerly direction. Individuals from northern areas like Lincoln and Natchitoches Parishes have distinct, but only slightly elevated, ridges that are either linear or angle slightly laterad toward the distal corner. In southern Louisiana the rim is distinctly longer at this corner and therefore obviously slanted in this direction. This variant extends into western Louisiana and eastern Texas, and in many individuals the medial corner is additionally prolonged into a papilla or short digitiform projection (Fig. 80). As with males, females are more variable in Texas than in Louisiana, and the overall picture in both states is extremely complex when one considers both sexes. Conclusions based on one sex are contradicted by the other, and in general female variation traverses the boundaries between male forms. I therefore regard *amplus* as a single highly variable species with three principle male morphs, which are characterized in the ensuing paragraphs along with lesser forms in Texas.

The first variant is represented by the holotype and occurs in northern Louisiana (Lincoln, Natchitoches, Desoto, Bienville, Red River, Sabine, and eastern Vernon parishes), extends across the Sabine River into Harrison County, Texas, and occurs sporadically to the west in Texas (Wood, Anderson, Tyler, and to a lesser extent Nacogdoches counties). In this form (Fig. 73), the aperture sides are moderately high and lean well over the opening at division point; the inner lateral margin extends downward or dorsad into the opening, and the outer lateral margin flares moderately laterad, all combining to form a distinct closed pouch. In addition to the rim, females in this area display a variable indentation on the medial valvular surface that is greater in individuals from the northern periphery of the third male variant, thus constituting another trait traversing a boundary between male forms.

The second male variant (Fig. 76) occurs to the south in Evangeline, Jefferson Davis, and Iberia parishes Louisiana. Here the sides of the aperture are more strongly elevated and upright from the anterolateral corner to division point. The outer lateral margin does not angle as strongly laterad and in some specimens is nearly colinear with the anterior part of the sides. The inner lateral margin is directed downward, and the net effect is a shallower pouch that is virtually absent from a few males. A similar form occurs in Montgomery County, Texas, and one in Nacogdoches County is intermediate between this and the first morph.

The third variant occurs in western Louisiana (western Vernon, Beauregard, Calcasieu, and Cameron parishes) and eastern Texas (Shelby, Jasper, Rusk, Smith, Polk, Houston, Grimes, Chambers, Galveston, and Harris counties) where it intermixes with the other two forms. Here the sides rise gradually to division point, which leans strongly mediad over the opening (Fig. 77). The inner lateral

margin extends slightly inward into the opening before curving broadly dorsad, and the outer lateral margin angles moderately laterad, forming a deep, moderately open pouch. This morph intermixes in eastern Texas with the second variant and with that named *hamatilis* by Loomis (1969) (Fig. 78), in which the pouch is even deeper and more open because the outer lateral margin flares strongly laterad and the inner margin extends submediad into the opening before curving dorsad. Thus, although the sides do not lean strongly over the opening, the pouch is still broad and deep because of the initial invagination of the inner lateral margin. As noted by Loomis (1969), this variant also possesses a sclerotized hook on the anterior surfaces of the prefemora on the 7th and 9th legs (Fig. 79). This type of aperture is known from three widely separated localities in Angelina, Panola, and Mason counties, the latter sites respectively about 66 miles north and 280 miles west of the first. The Mason County record represents an apparently allopatric population in the midst of *melacis,* some 200 miles west of the closest known site of either *amplus,* the *varius* group, or the *Kewanius* lineage. In the area of eastern Texas occupied by the third variant, the valvular rim in females slopes strongly mediad, usually culminating in a variably papillate to digitiform projection on the distal corners (Fig. 80), the projection tending to be longer and more digitiform to the south. However, some females in this area lack papillae and exhibit slanted rims. The form named *hamatilis* is recognizably different, but the situation with females and sympatry with other males indicates that it is merely one variant of a highly variable species. Consequently, *hamatilis* is a junior synonym of *amplus.*

Ecology. — The male I collected in July 1980 in Harrison County, Texas, the wrong season for eurymerodesmids, consisted of loose exoskeletal rings without appendages and was identified from the aperture configuration. The segments were found under leaf litter beside a building at Caddo Lake State Park. The specimens from Harris County were discovered under logs beside a trail in a predominantly pine habitat at Memorial Park, Houston. Habitat notations on other vial labels are as follows: under logs and boards in a bottomland meadow adjacent to a pine-hardwood forest (Red River Par., LA), in a rotting shed (Sabine Par., LA), at a plant nursery (Jefferson Davis Par., LA), under sawdust (Vernon Par., LA), under a log (Nacogdoches Co., TX), in a greenhouse (Smith Co., TX), and on a prairie (Chambers Co., TX). The sample from near Steinhagen Lake, Tyler County, Texas, was discovered by ultraviolet light at night, apparently flourescing.

Distribution. — Louisiana from the Mississippi River and the Atchafalaya Bayou to the middle Trinity and lower Brazos Rivers in eastern Texas, with an allopatric population 200 miles to the west on the eastern periphery of the Edwards Plateau in Mason County (Figs. 54, 211-212). Specimens were examined as follows:

LOUISIANA: *Lincoln Par.,* Ruston, M, F, November 1951, W. J. Harmon (AMNH) and 4M, juv., 2 January 1953, F. L. Afeman (FSCA) TYPE LOCALITY. *Bienville Par.,* Castor, 2M, 21 November 1954, J. E. Sublette (FSCA). *Natchitoches Par.,* Creston, 14M, 8F, 27 February-5 May 1915, K. P. Schmidt (MCZ); Grand Ecore, M, 26 October 1934, J. E. Sublette (FSCA); Natchitoches, M, 13 November 1953, B. Stanberry (FSCA) and M, 25 February 1954, J. E. Sublette (FSCA); and Kisatchie, M, F, 30 October 1954, W. J. Harmon (FSCA). *Avoyelles Par.,* Evergreen, F, 23 December 1965, M. Kordisch (FSCA). *Red River Par.,* 3.7 mi. NW Coushatta, 4M, 3F, 10 April 1971, P. J. Kinnick (FSCA); and Coushatta, M, 28 November 1953, Bamburg (FSCA). *Desoto Par.,* along US hwy. 171, 2.5 mi. N Mansfield, 4M, 13 March 1966, R. E. Tandy (FSCA). *Sabine Par.,* Hodges Garden, along US hwy. 171 N of Sandel, 2M, 7F, juv., 26 March 1965, R. E. Tandy, G. E. Gates (FSCA). *Vernon Par.,* unknown locality, F, 17 June 1956, J. E. Sublett (FSCA); LA hwy. 111, 1.9 mi. N. jct. LA hwy. 464, F, 19 February 1966, R. E. Tandy (FSCA); 2.4 mi. ENE Pitkin, 3M, 3F, 20 February 1966, R. E. Tandy (FSCA); near Sabine R. on LA hwy. 8, 4M, 2F, 25 March 1965, R. E. Tandy, G. E. Gates (FSCA); and along LA hwy. 464, 11.5 mi. SSW Caney, M, 19 February 1966, R. E. Tandy (FSCA). *Allen Par.,* West Bay Game Area, F, 2 October 1965, L. D. Wilson (FSCA). *Beauregard Par.,* US hwy. 190 at Sabine R., F, 30 April 1966, R. E. Tandy (FSCA); and DeRidder, 8M, 6F, 20 March, 17 October, and 9 December 1969, H. Rhame (FSCA); and 5 mi. S DeRidder, 6M, 3F, 22 juvs., 10 December 1969, H. Rhame (FSCA). *Evangeline Par.,* Lake Chicot, F. 20 March 1965, M. Kordisch (FSCA); 2.5 mi. S Chicot St. Pk., M, 30 January 1968, E. D. Kaiser (FSCA); and Boggs Bayou, 2.7 mi. W jct. LA hwys. 106 and 13, M, F, 9 January 1966, R. E. Tandy (FSCA). *Iberia Par.,* Avery Island, M, F, juv., 7 April 1974, N. B. Causey (FSCA). *Acadia Par.,* I-10 at Mermentan R., 2F, 26 September 1965, R. E. Tandy (FSCA).

Jefferson Davis Par., Elton, 14M, 11F, 29 November 1964 and 1 March 1965, C. Steal (FSCA). *Calcasieu Par.,* Lake Charles, M, juv., 15 April 1965, and 4M, 4F, 28 April 1967, M. Kordish (FSCA); Sulphur, 4M, 4F, 22 February 1965, collector unknown (FSCA); and 10 mi. W Lake Charles, M, F, 18 November 1964, M. Kordish (FSCA). *Cameron Par.,* 5 mi. W Holly Beach, M, 29 April 1962, K. Arnold (FSCA).

TEXAS: *Harrison Co.,* nr. Waskom, 2F, 25 March 1962, N. B. Causey (FSCA); and Caddo Lake St. Pk., M (exoskeletal fragments), 11 July 1980, R. M. Shelley (NCSM). *Panola Co.,* Carthage, 3M, 3F, 10 March and 24 November 1962, L. P. Hull (FSCA). *Shelby Co.,* Paxton, 13M, 8F, date and collector unknown (FSCA). *Wood Co.,* Alba, 5M, 3F, 2 juvs., 7 February 1932, collector unknown (NMNH). *Smith Co.,* Tyler, 2M, 28 December 1964, T. C. Stewart (FSCA). *Rusk Co.,* along US hwy 259, 5 mi. N Mt. Enterprise, M, 19 November 1967, T. C. Stewart (SFAU); along FM 836, 3 mi. N New Salem, 4M, 3F, 17 November 1967, T. C. Stewart (FSCA); along FM 834, 3 mi. S New Salem, F, 3 juvs., 17 November 1967, T. C. Stewart (SFAU); and Lufkin, juv. M, 22 May 1940, S. and D. Mulaik (NMNH). *Anderson Co.,* Palestine, 3M, 3F, 3 juvs., 26 January 1962, J. O'Keefe (FSCA). *Houston Co.,* Crockett, 6M, 3F, 4 December 1961, L. Heard (FSCA). *Nacogdoches Co.,* Nacogdoches, 10M, 6F, November 1931, collector unknown (NMNH) and M, 11 October 1966, T. C. Stewart (SFAU); and Stephen F. Austin Forest, 2M, 16 March 1968, J. Reddell (FSCA). *Angelina Co.,* 8 mi. N Zavalla, near Sam Rayburn Res., 4M, F, 4 juvs., 23 April 1967, J. C. Loomis (NMNH, FSCA); and county airport, F, 13 October 1966, J. A. Kelgey (SFAU). *Jasper Co.,* Jasper, 26M, 32F, juv., 15 January-25 March 1962, J. DuRard (FSCA). *Tyler Co.,* Woodville, 12M, 14F, 8 juvs., 22 February 1962, R. Timbrook (FSCA); and along US hwy. 190 at Steinhagen L., 25M, 4F, 20 October 1985, J. C. and J. E. Cokendolpher (NCSM). *Polk Co.,* Dallardsville, 2M, juv., 24 February 1962, J. P. Kennedy (FSCA). *Grimes Co.,* Navasota, 7, January 1931, collector unknown (NMNH) and M, F, 5 juvs., 2 December 1961, W. Watkins (FSCA). *Montgomery Co.,* Conroe, 5M, 2 juvs., 10 March 1963, B. Ray (FSCA). *Harris Co.,* Houston, F, 20 December 1930, collector unknown (NMNH) and Memorial Pk., M, 2F, 18 February 1986, R. M. Shelley (NCSM). *Chambers Co.,* Smith Point, 4M, 2F, 3 November 1918, Hansen and Barber (NMNH). *Galveston Co.,* La Marque, 4M, 9F, 7 juvs., date unknown, W. A. Benton (FSCA); and Galveston Island, 2M, F, 1870, W. Julich (MCZ). *Mason Co.,* 1 mi. NE Mason, 3M, 8 November 1964, J. Reddell (FSCA).

Remarks. — The specimens from an unspecified site in Louisiana and reported by Brolemann (1895) as *Leptodesmus hispidipes* are *amplus.* This sample consists of 11 males and 2 females and is housed at the MNHP. Brolemann (1900) did not mention a locality, but I believe he was referring to this sample when he proposed *Fontaria (Eurymerodesmus) hispidipes.* The specimens from Creston, Natchitoches Parish, Louisiana, which Chamberlin (1918) also recorded as *Leptodesmus hispidipes,* are mostly *amplus,* though they also contain a male of *birdi.* An *amplus* male from this site measured 29.1 mm long, 4.3 mm wide, W/L ratio 14.8%. Finally, the records of *E. hispidipes* by Stewart (1969) from Angelina, Nacogdoches, Rusk and Smith, counties, Texas, also refer to *amplus,* and since his records from Sabine, Shelby, and Upshur counties lie within the range, they are shown as literature records of *amplus* in figures 54 and 212.

Eurymerodesmus newtonus Chamberlin
Figs. 54, 83-88, 211

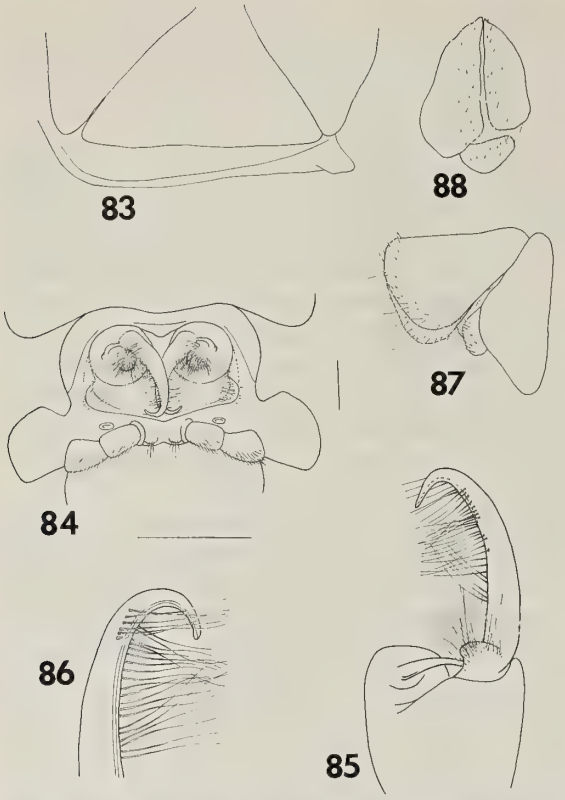
Eurymerodesmus newtonus Chamberlin, 1942a:5, pl. 2, fig. 14. Chamberlin and Hoffman, 1958:80.

Eurymerodesmus bentonus Causey, 1950a:268-270, fig. 5. Chamberlin and Hoffman, 1958:78. **NEW SYNONYMY.**

Type specimens. — Male holotype and two female paratypes (NMNH) collected by L. Hubricht, 29 April 1936, in the Boston Mountains, 1.2 mi. S Jasper, Newton Co., AR. The head and pregonopodal segments of the holotype are missing, and the male description is therefore based on the specimen from Monte Ne, Benton County, Arkansas, whose gonopods and aperture are virtually identical.

Diagnosis. — A moderate-size species; males characterized by moderate-size mandibular projection; sides of aperture divided, with moderately open caudolateral pouches; telopodite long; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, uncinate; prefemur with many hairs arranged continuously along inner surface; cyphopod valves of females not modified, without projections; receptacle moderate-size, sides curving partly around operculum.

Color in Life. — Paranota orange; metaterga dark olive with orange stripes along caudal margins connecting paranotal markings; collum with orange stripes along both anterior and posterior borders



Figs. 83-88. *Eurymerodesmus newtonus.* 83, projection of right mandible of male from Benton Co., AR, lateral view. 84, aperture and gonopods *in situ* of male from Washington Co., AR, ventral view. 85, left gonopod of holotype, lateral view. 86, telopodite of left gonopod of male from Benton Co., AR, medial view. 87, left cyphopod of female paratype, caudal view. 88, the same, medial view. Scale line for fig. 84 = 1.00 mm. Line for other figs. = 0.35 mm for 85, 0.40 mm for 83 and 87-88, and 0.50 mm for 86.

(Causey 1950a). Chamberlin (1942a) reported preserved coloration and noted stripes.

Male from Monte Ne, Benton Co., AR. Body highly fragmented, length unmeasurable, maximum width 4.8 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.7 mm, interantennal isthmus 0.9 mm. Antennae reaching back to caudal end of 2nd tergite; antennomeres becoming progressively more hirsute distad, relative lengths 2>3>5>4>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 9-9, labral about 14-14. Projection of mandibular stipes moderately long, apically narrowly rounded (Fig. 83).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum basally, flattened distad; posterior corners rounded through segment 6, blunt on 7-12, becoming progressively more acute posteriorly.

5th sternum with minute lobes between 4th legs and broader elevated areas between 5th legs; 6th sternum with short, paramedian knobs between both leg pairs. Postgonopodal sterna with minute, widely segregated lobes between 9th legs; remaining sterna generally flat and plate-like, with variable transverse impressions originating between leg pairs and moderate hair patches subtending coxae. 2nd legs absent, coxal configuration unknown. Prefemoral lobes broadly rounded, extending through segment 11.

Gonopodal aperture (Fig. 84, not this specimen) ovoid, with partly open caudolateral pouches, slightly indented anteriad at midline, 1.3 mm wide and 0.4 mm long at maxima, outline of apparatus irregularly hexagonal; anterior indentation short, broad, apically rounded; sides curving slightly mediad and leaning slightly over opening, rising slowly and continuously to division point distal to midlength, inner lateral margin very short, curving immediately into inner caudal margin, outer lateral margin flaring slightly sublaterad, not leaning over opening, curving and dropping rapidly to metazonal surface just before caudolateral corner, forming moderate, open pouch with inner margin, rims slightly emarginate; inner caudolateral corner indistinct, smoothly curved continuation of inner lateral margin; outer caudolateral corner broadly curved; inner caudal margin angling caudad, outer third slightly elevated; outer caudal margin angling slightly caudad, more so in midline; anterior margin glabrous, sides with scattered hairs arising from rims beginning along elevation before division point, with short marginal hairs at caudolateral corners and slight tufts from within pouches. Gonopods *in situ* (Fig. 84, not this specimen) with telopodites angling across midline and crossing opposite member, extending to caudal margin then curving laterad, lying nearly completely over and under each other, tips directed dorsolaterad. Gonopod structure as follows (Figs. 85-86): Telopodite terminating just before level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, stem curving gently and evenly dorsad for most of length, more so distad, expanding slightly near midlength, narrowing distad, with two rows of continuous, regularly spaced hairs along inner margin and distomedial tuft of about 6 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, uncinate, curving strongly dorsolaterated, poorly demarcated from, and smoothly continuous with, prefemur, narrowing smoothly and continuously to subacuminate tip.

Female paratype. — Length 27.0 mm, maximum width 4.2 mm, W/L ratio 15.6%. Agreeing essentially with holotype in somatic features, with following exceptions: Mandibular stipes with short, rounded projection. Sterna flat, with only a few sparse hairs on anterior segments, glabrous thereafter.

Cyphopodal aperture elliptical, caudal margin indented slightly mediad, sides slightly elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely in aperture, central groove visible in opening. Valves (Figs. 87-88) moderately large, unequal, anterior one slightly larger, without lobes or projections, moderately hirsute distad. Receptacle oriented dorsoventrad at bases of valves, forming right angle with latter, curving partly around base of operculum, glabrous. Operculum relatively large, located under valves, partly shielded on anterior and posterior sides by receptacle.

Variation. — The holotype gonopods lack the characteristic distomedial tuft of prefemoral hairs that is present on other males. The male from Washington County exhibits a slight distal swelling on the outer prefemoral margin.

Distribution. — Known definitely from only three counties in the northwest corner of Arkansas (Figs. 54, 211). Specimens were examined as follows:

ARKANSAS: *Newton Co.,* Boston Mts., 1.2 mi. S Jasper, M, F, 29 April 1936, L. Hubricht (NMNH) TYPE LOCALITY. *Benton Co.,* Monte

Ecology. — The material from Benton County reported by Causey (1950a) was collected in predominantly oak woods at the base of a north-facing slope.

Ne, M, 2F, 19 November 1949, N. B. Causey (ANSP, FSCA). *Washington Co.,* Cove Creek Valley, M, Spring 1956, M. Hite (FSCAQ).

Remarks. — According to Chamberlin (1942a), the type series of *newtonus* contained the male holotype and three females, two of which are lost.

Causey (1950a) reported collecting numerous specimens of *newtonus* along with *birdi* at Blue Springs, Carroll County, Arkansas. This material also is lost, but the site is within the area circumscribed by the three known counties and thus is plausible for the species. It is shown as a literature record in figures 54, 211.

One of the specimens Causey (1950a) reported from Benton County is an "intersex," labeled a "hermaphrodite" in the vial, with typical cyphopods, gonopods, and genital apertures at the normal locations. The specimen is present in the FSCA and is a functional female with eggs and the female paranota, sterna, and legs. I interpret the gonopods as a developmental accident reflecting the ability of appendages on anterior segments in both sexes to become either legs or gonopods depending on genetic signals. I (1977) summarized examples of this phenomenon in the Xystodesmidae, and it is also exhibited by an accessory gonopod on a male of *b. birdi.* Such accidents are rare in females, and it is noteworthy that the gonopods are at the normal location, the anterior position of segment 7.

Eurymerodesmus oliphantus Chamberlin
Figs. 54, 89-95, 211

Eurymerodesmus oliphantus Chamberlin, 1942a:6, pl. 2, fig. 15. Chamberlin and Hoffman, 1958:80.

Eurymerodesmus hispidipes: Causey, 1950a:267-268, figs. 1-4; 1952b, fig. 2. Chamberlin and Hoffman, 1958:191 (in part).

Type specimens. — Male holotype and female allotype (NMNH) collected by L. Hubricht, 10 April 1936, 15 mi. SW Oliphant, Jackson Co., AR.

Diagnosis. — A small to moderate-size species; males characterized by long mandibular projection; sides of aperture divided, with widely open caudolateral pouches; telopodite long; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females not modified, without projections; receptacle moderate-size, sides curving partly around operculum.

Color in Life. — Paranota red; metaterga black with broad, red stripes along caudal margins connecting paranotal markings; collum with red stripes along both anterior and posterior borders (Fig. 89). Chamberlin (1942a) and Causey (1950a) also noted the striped pattern in preserved specimens.

Holotype. — Body highly fragmented, length unmeasurable, maximum width 3.8 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.6 mm, interantennal isthmus 0.9 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres $2>3>4=5=6>1>7$. Genae without impressions. Facial setae with only clypeal about 8-8, and labral, about 12-12, series. Process of mandibular stipes long, bowed inward, narrowly rounded apically (Fig. 90).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-10, becoming progressively more acute caudally.

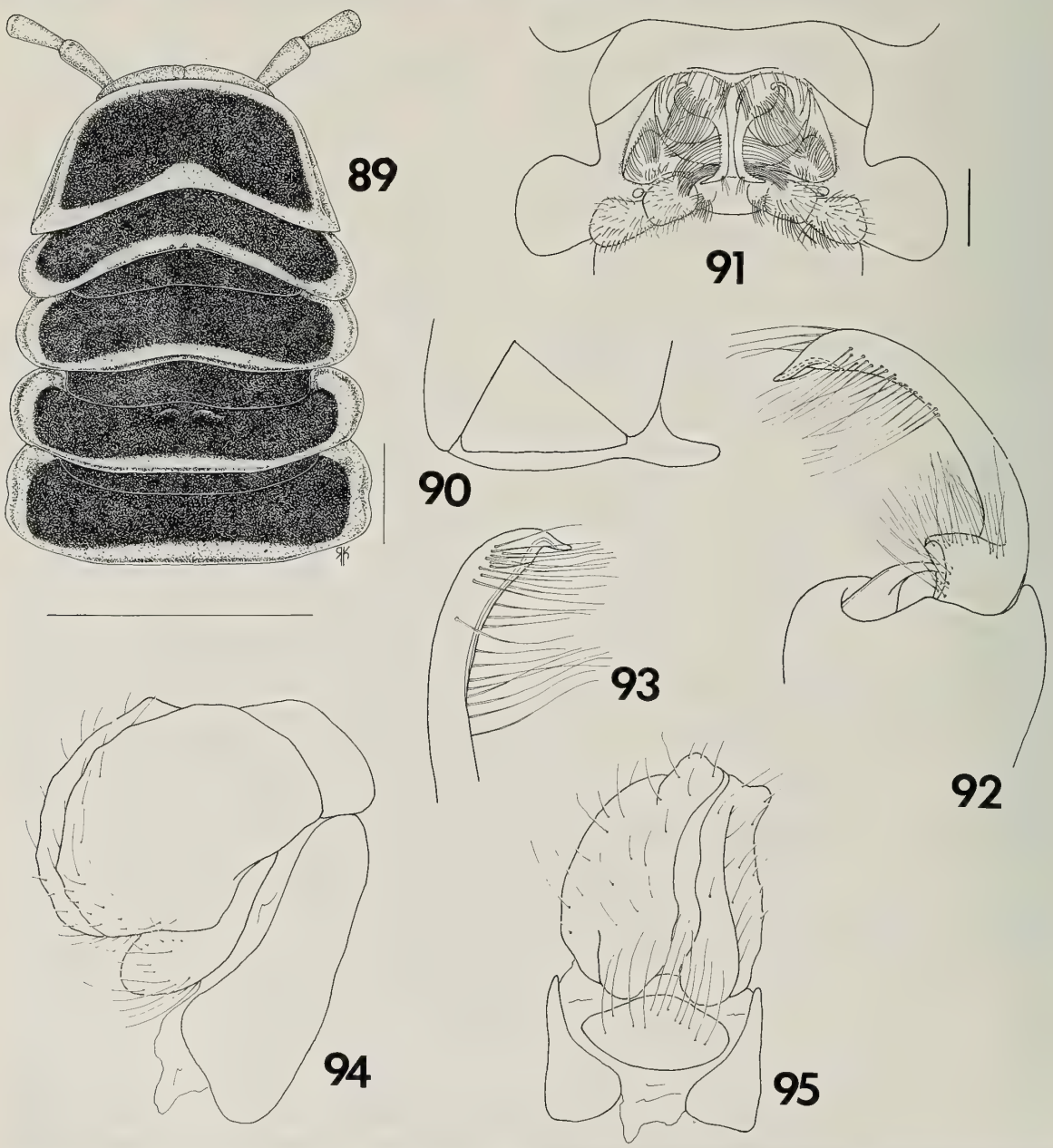
5th sternum with dense hirsute patches adjacent to leg coxae, not elevated; 6th sternum with low, elevated, areas adjacent to leg coxae. Postgonopodal sterna with deep central impression and low, elevated, hirsute areas between 9th legs; remaining sterna generally flat and unmodified, with hair patches adjacent to leg coxae, becoming progressively sparser caudally. 2nd coxa with broadly rounded, subequal anterior and posterior lobes. Prefemoral lobes extending through segment 10.

Gonopodal aperture (Fig. 91, not this specimen) ovoid, with open, caudolateral pouches and short, broad anterior indentation, 2.3 mm wide and 0.9 mm long at maxima, outline of apparatus trapezoidal; anterior indentation short, broad; sides curving mediad to division point, upright, not leaning over opening, rising progressively to division point at midlength, inner lateral margin continuing curved contours, extending inward, dropping abruptly, and curving smoothly into inner caudal margin, outer lateral margin well separated from inner, flaring strongly and obliquely caudolaterad, lowering progressively to metazonal surface at caudolateral corner, forming broad, deep, open pouch with inner margin, rims of anterolateral margins smooth, those of inner and outer margins slightly irregular; inner caudolateral corners indistinct, broadly rounded; outer caudolateral corners broadly triangular, about 45°; inner caudal margin curving slightly, dropping rapidly to metazonal surface, and extending sublinearly across midline; outer caudal margin curving slightly along anterior surfaces of coxal condyles and continuing as faint line across midline; margins densely and irregularly hirsute, with long hairs arising sporadically from anterior and lateral rims, particularly along anterior indentation and from outer surface of outer lateral margin, and overhanging opening, also with dense tufts of short hairs arising from within pouches, caudal margins glabrous. Gonopods *in situ* (Fig. 91, not this specimen) with telopodites abutting or lying parallel to each other in midline, curving laterad over caudal margins and terminating over 9th coxal condyles, tips directed dorsolaterad. Gonopod structure as follows (Figs. 92-93):

Telopodite terminating well before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, leaning over coxa, narrowing slightly to around midlength then expanding, widest at distal extremity, with numerous long hairs arranged continuously in two rows along inner margin and distomedial tuft of about 10 hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, angling dorsolaterad, poorly demarcated from, and smoothly continuous with, prefemur, narrowing rapidly near midlength to acuminate, slightly bisinuate tip.

Allotype. — Length 28.4 mm, maximum width 3.8 mm, W/L ratio 13.4%. Agreeing closely with holotype in somatic features, with following exceptions: Mandibular stipes with short, broadly rounded projection. Sterna flat, nearly glabrous, with at most only an occasional scattered hair.

Cyphopodal aperture subrectangular, sides elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely in aperture, distal surface of anterior valve visible in opening. Valves (Figs. 94-95) relatively large, unequal, anterior valve larger, extending slightly above and overlying caudal valve, moderately hirsute. Receptacle located laterad at bases of valves, relatively narrow, sides curving partly around operculum. Latter large, located under free, dorsomedial side of valves.



Figs. 89-95. *Euerymerodesmus oliphantus.* 89, segments 1-5 of male from Jackson Co., IL, dorsal view. 90, right mandibular process of holotype, lateral view. 91, aperture and gonopods *in situ* of male from Jackson Co., IL, ventral view. 92, left gonopod of holotype, lateral view. 93, telopodite of the same, medial view. 94, left cyphopod of allotype, caudal view. 95, the same, medial view. Scale lines for figs. 89 and 91 = 1.00 mm. Line for other figs. = 0.60 mm for 90 and 92, 1.00 mm for 93-95.

Variation. — Measurements of a male from White County, Arkansas, adjacent to Jackson County, are length 23.7 mm, maximum width 3.7 mm, W/L ratio 15.6%.

The most notable variation is the marked reduction in hirsuteness in the southernmost males from Jackson and White counties, Arkansas. All other specimens are extremely hairy, particularly inside the pouches and along the rim and outer surfaces of the outer lateral margins; hence one such male was used to depict the aperture configuration and the *in situ* gonopod arrangement (Fig. 91) rather than the holotype.

The aperture configurations are very similar throughout the range. In males from White County, Arkansas, and Phelps, Pulaski, and St. Louis counties, Missouri, the flare extends more obliquely laterad and tends to lean over the pouch, thus forming a cavity beneath the outer lateral margin from which more hairs arise. The angle of slope of the inner caudal margin can vary from gradual as in the holotype to steep as in males from Pope County, Illinois. The distance between the inner and outer lateral margins, or the rate at which they diverge, also varies, and males in which this distance is greater possess a cavity with hairs beneath the division point.

In situ the telopodites may be parallel (Fig. 91) or they may cross each other basally in the midline of the aperture (at the bases of the prefemora) and again distad at the bases of the acropodites above the sternum between the 9th legs. In northern males the acropodite is not apically bisinuate.

The female from St. Louis County, Missouri, the only adult female collected aside from the allotype, agrees with the latter in that the anterior valve is larger than the caudal one.

Ecology. — According to vial labels, the males from Pope County, Illinois, were encountered under rocks. I discovered that from Jackson County, Illinois, deeply buried in a rotting oak stump in the Shawnee National Forest.

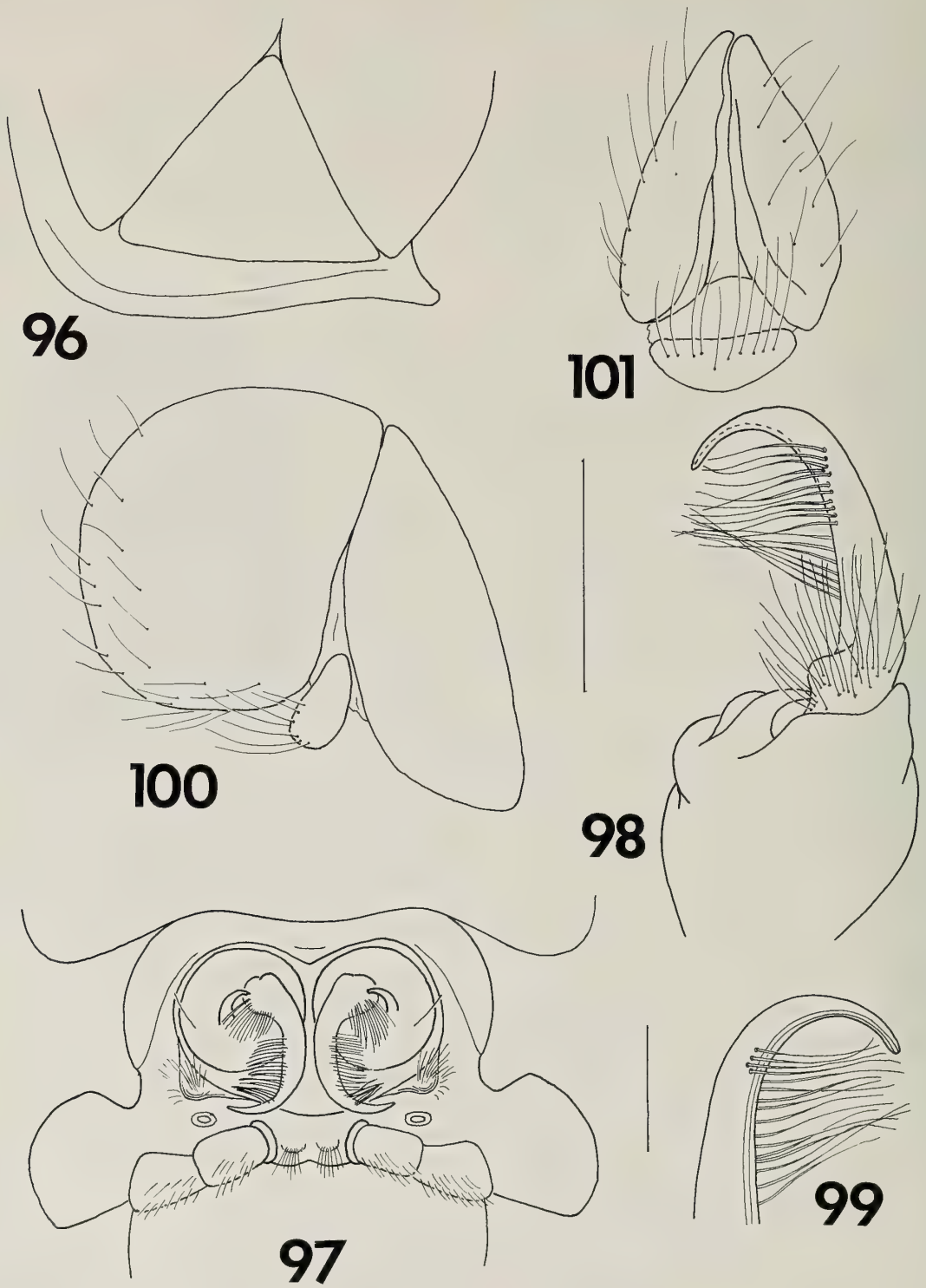
Distribution. — The eastern Ozark Plateau of Arkansas and Missouri and the western Interior Low Plateaus of southern Illinois (Figs. 54, 211). The available samples come from four areas, and field work is needed in the lacunae to determine if they connect. Specimens were examined as follows:

ILLINOIS: *Jackson Co.,* 1.5 mi. W Pomona, along rd. to Pomona Nat. Bridge, M, 15 April 1984, R. M. Shelley (NCSM). *Johnson Co.,* Ferne Clyffe St. Pk., 2M, 27 October 1967, J. A. Beatty (WAS). *Johnson/Pope cos.,* 3 mi. E Ozark, M, 11 March 1950, P. W. Smith (FSCA). *Pope Co.,* Dixon Springs, 2M, 3 april 1948, Smith, Burks, and Stannard (FSCA, ILNHS).

MISSOURI: *St. Louis Co.,* Ranken, exact location unknown, M, F, 2 April 1933 and 17 March 1935, E. P. Meiners (UMO). *Phelps Co.,* 3 mi. NE Rolla, M, 17 April 1965, G. L. Rotramel (ILNHS); and 4 mi. S Jerome, Gable Springs Cv., M, 4 April 1979, J. E. Gardner (NCSM). *Pulaski Co.,* 8 mi. WSW Edgar Springs, Ryden Cv., M, 3 March 1979, J. E. Gardner (NCSM).

ARKANSAS: *Independence Co.,* 1.3 mi. W Cushman, 2M, 2 juv. F, 5 March 1973, R. M. Blaney (FSCA). *Jackson Co.,* 1.5 mi. SW Oliphant, M, F, 10 April 1936, L. Hubricht (NMNH) TYPE LOCALITY. *White Co.,* Russell, M, 25 December 1952, C. Pennington (FSCA).

Remarks. — The record of *hispidipes* from Dixon Springs, Pope County, Illinois, by Causey (1950a), subsequently cited by Chamberlin and Hoffman (1958), actually refers to *oliphantus.* Since the types of *hispidipes* are from an unknown site in Illinois (Wood 1864, 1865) and *oliphantus* is the only species known from forested areas in the southern part of the state, it is frequently misidentified as the former. For example, I originally assumed that my specimen from Jackson County was *hispidipes,* but two species occur in this state. The prior confusion is understandable since no one has attempted to illustrate the apertures of the *hispidipes* syntypes, which have resided at the NMNH for a century and a quarter. To my knowledge they have not been examined since 1865, and in particular Causey (1950a) missed a golden opportunity to establish the identity of *hispidipes* by examining and illustrating them. Instead, she mistakenly assumed that the male of *oliphantus* from Dixon Springs (ILNHS) was *hispidipes,* so named it, and illustrated the mandibular process, the 2nd coxa, the aperture, a gonopod from lateral, not ventral, view, and the sternal projections between the 9th legs, 8th by her count. The aperture drawing from the lateral perspective does not show the pouches and is meaningless, so none of these drawings are definitive. Causey (1952a) provided a ventral view of the aperture showing the pouches and again, erroneously, labeled it *hispidipes.* Subsequent confusion can be traced to these mislabeled drawings, and when I examined the types of *hispidipes,* I was shocked to view a different form. I surmise that *hispidipes* is more common in central Illinois, where there has been little recent collecting, whereas *oliphantus* is abundant in the



Figs. 96-101. *Eurymerodesmus elevatus*. 96, projection of right mandible of holotype, lateral view. 97, aperture and gonopods *in situ* of holotype, ventral view. 98, left gonopod of the same, lateral view. 99, telopodite of the same, medial view. 100, left cyphopod of female paratype, caudal view. 101, the same, medial view. Scale line for fig. 97 = 1.00 mm. Line for other figs. = 0.30 mm for 96, 0.40 mm for 98 and 100-101, and 0.50 mm for 99.

southern part of the state, in the mesic woodlands of the Shawnee National Forest.

Eurymerodesmus oliphantus is one of three species taken from caves, the others being *melacis* and *birdi*. As indicated later, *melacis* may seek refuge in caves, but *oliphantus* is surely an accidental species, since there is abundant, moist epigean habitat in the Ozarks.

Eurymerodesmus oliphantus has the largest, most open caudolateral pouches in the family, so much so that they alone are diagnostic for the species.

Eurymerodesmus elevatus, new species
Figs. 54, 96-101

Type specimens. — Male holotype and female paratype (FSCA) collected by W. W. Dowdy, 12 February 1966, on Neilhorn Place, Jefferson City, Cole Co., MO. Male paratype (NCSM) taken by same collector, 15 April 1965, on Lepage Place, Cole Co., presumably in Jefferson City.

Diagnosis. — A small to moderate-size species; males characterized by relatively short mandibular projection; sides of aperture divided, outer lateral margin rising beyond division point into cupped elevated lobe forming false pouch on inner surface; telopodite long; acropodite short, about 1/4 of the telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of female not modified, without projections; receptacle moderate-size, sides not curving around operculum.

Color in life. — Unknown.

Holotype. — Fragmented into three pieces, approximate length 19.2 mm, maximum width 3.2 mm, W/L ratio 16.7%.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.3 mm, interantennal isthmus 0.8 mm. Antennae reaching back to middle of 3rd tergite, relative lengths of antennomeres 2>3>5>6>4>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 1-1, clypeal about 7-7, labral about 16-16. Process of mandibular stipes relatively short, subtriangular, apically blunt (Fig. 96).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum; posterior corners rounded through segment 10, blunt on 13-15, becoming progressively more acute caudally.

5th sternum with elevated flattened areas between 4th legs and larger paramedian knobs between 5th; 6th sternum with broad, elevated areas between both leg pairs. Postgonopodal sterna with slightly elevated, widely segregated hirsute areas between 9th legs; remaining sterna generally flat and unmodified, with variably impressed transverse grooves originating between leg pairs and hair patches adjacent to leg coxae, becoming progressively sparser caudally. 2nd coxa with short, broadly triangular anterior, and minute caudal, lobes. Prefemora with broad lobes on outer surfaces of legs through segment 10.

Gonopodal aperture (Fig. 97) broadly ovoid, with open caudolateral pouches and short, broad anterior indentation, 1.6 mm wide and 0.7 mm long at maxima, outline of apparatus subrectangular; anterior indentation short, broad, subacuminate; sides divided, essentially upright, not leaning over opening, rising continuously from anterolateral corner to peak on outer lateral margin at caudolateral corner beyond division point, latter caudal to midlength, inner lateral margin continuing curvature of anterior part of sides, blending smoothly into inner caudal margin, outer lateral margin rising continuously into broad, elevated lobe at caudolateral corner, not flaring laterad, cupped with slight cavity on inner surface in conjunction with outer caudal margin, rims of anterior lateral margins slightly irregular, becoming more so on elevation; inner caudolateral corners smoothly curved, indistinct, continuous with inner lateral margin; outer caudolateral corners relatively sharp, nearly a right angle; inner caudal margin smoothly continuing curvature of sides, merging with outer caudal margin well before midline, at about 1/3 length; latter dropping rapidly from caudolateral corner to level of metazonum, angling inward and merging with inner caudal margin, the two then continuing as single, smoothly curved caudal margin across midline; anterior margin and anterior halves of sides essentially glabrous, a single hair arising from rim of latter, more hairs arising from rim of outer caudal margin on elevation beyond division point, with additional short hairs on outer surface of elevation and moderate tuft in pouch, caudal margin glabrous. Gonopods *in situ* (Fig. 97) with telopodites approaching each other in midline then curving broadly laterad across caudal margin, terminating over 9th coxal condyles, apices directed sublaterad. Gonopod structure as follows (Figs. 98-99): Telopodite extending slightly beyond level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, bowed for most of length, more so distad, narrowing smoothly and continuously, with two rows of continuous, evenly spaced hairs along inner margin, angling outward distad, and distomedial tuft of four hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, poorly demarcated from, and smoothly continuous with, prefemur, smoothly continuing curvature of distal part of latter basally, flattening at midlength, becoming uncinate distally, narrowing continuously to acuminate tip.

Female paratype. — Body fragmented, length approximately 25.3 mm, maximumn width 3.9 mm, W/L ratio 15.4%. Agreeing essentially with holotype in somatic features, with following exceptions: Mandibular stipes with minute, rounded, process. Sterna flat and nearly glabrous, with only a few scattered hairs.

Cyphopodal aperture subrectangular, sides slightly elevated above metazonal surface, caudal margin with moderate indentation at midpoint. Cyphopods *in situ* with edges of valves and tip of receptacle visible in aperture. Valves (Figs. 100-101) oriented transversely in aperture, relatively small, subequal, without projections or modifications, lightly hirsute on medial side. Receptacle located laterad to valves, relatively small, glabrous, sides not curving around operculum. Latter small, located under free, dorsal, side of valves.

Male paratype. — The male paratype agrees with the holotype in all particulars.

Variation. — The other Cole County males and females agree closely with the holotype and paratype, except that the gonopods *in situ* may cross

in the midline of the aperture and again over the caudal margin, or lie over and under one another in the midline. In the Morgan County male, the outer lateral margin is more strongly elevated and flares slightly laterad, thus forming a higher and slightly deeper pouch.

Ecology. — According to the vial label, the holotype and female paratype were collected "in soil." The male from the flood plain in Cole County was taken from the "first inch" presumably of the soil or leaf litter. There are no indications whether these sites were in forest, pasture, or other environments.

Distribution. — Known only from two counties in central Missouri (Fig. 54), the distance between known sites being only about 50 miles. Specimens were examined as follows:

MISSOURI: *Cole Co.,* Jefferson City, Neilhorn Pl., M, F, 12 February 1966, W. W. Dowdy (FSCA) TYPE LOCALITY; Lepage Pl., probably near Jefferson City, M, 15 April 1965, W. W. Dowdy (NCSM); flood plain without further data, M, 19 January 1968, W. W. Dowdy (FSCA); and along US hwy 54 in southern Cole Co., M, 2F, 25 October 1965, W. W. Dowdy (FSCA). *Morgan Co.,* Versailles, M, 12 April 1959, D. Zusteg (FSCA).

Remarks. — The specimens of *elevatus* were either broken when I obtained them or fragmented upon handling. All measurements are therefore approximations.

The cavity formed by the elevated outer lateral and caudal margins, the cupped inner surface of the elevation, is convergent with that of *impurus* in that the inner lateral margin forms the floor instead of the inner edge. It differs from the true pouches of other species in the *varius* group, but the hair tuft in the cavity and the uncinate acropodite, similar to that of *newtonus,* indicate that *elevatus* properly belongs here.

The **Simplex** Group

The *simplex* group includes forms with short acropodites that are discontinuous with, and strongly demarcated from, the prefemur in all populations. It contains the fourth oldest species, *simplex.* The acropodite may be subterminal, with the distal extremity of the prefemur overhanging and extending beyond it, or narrowly terminal arising exclusively from the inner prefemoral margin, the outer surface of which projects above the junction and may be expanded or clavate but does not extend distad beyond the origin of the acropodite. Apertures vary, some having divided lateral margins and pouches, as in *simplex, paroicus,* and *crassatus,* others having undivided sides and triangular lobes on the caudal margin as found in *birdi,* for example *polkensis* and *pulaski,* and still others exhibiting undivided sides without lobes, for example *caesariatus* and *serratus.* The *simplex* group occurs sporadically from Florida to Louisiana and western Arkansas. Most components are widely segregated, and *serratus* even has allopatric populations some 700 miles apart. Consequently, a number of undiscovered forms probably exist, particularly in southern Arkansas, northern Louisiana, and western Mississippi.

As stated previously, *varius,* with discontinuous acropodites in *v. christianus,* links the *simplex* and *varius* groups into a single natural assemblage. For convenience I separate them based on the degree of differentation between the acropodite and prefemur, and the relative number of populations displaying this trait.

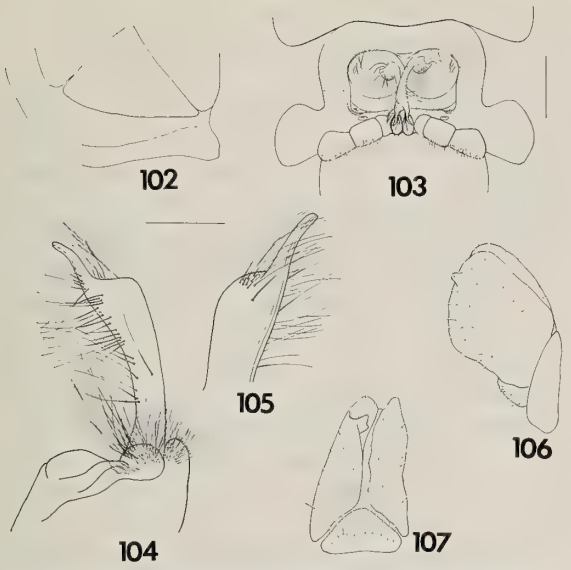
Components: simplex Chamberlin; *paroicus* (Chamberlin); *pulaski* (Causey); *polkensis* (Causey); *caesariatus,* new species; *crassatus,* new species; and *serratus,* new species.

Eurymerodesmus simplex Chamberlin
Figs. 54, 102-107, 211

Eurymerodesmus simplex Chamberlin, 1920:98-99. Attems, 1938:187.
Kewanius simplex: Chamberlin and Hoffman, 1958:82.

Type specimen. — Male holotype (MCZ) and one male and one female paratype (NMNH) collected by H. E. Hubert on an unknown date in 1918 from an unknown locality in Louisiana. The labels in the vials and Chamberlin (1920) reported New Orleans as the type locality, but Chamberlin and Hoffman (1958) stated that the site was "probably near" this city and that no definite localities were known. Two other eurymerodesmids, *birdi planus* and *varius christianus* are known from New Orleans and environs, but the only definite sites for *simplex* are in Evangeline and Rapides Parishes, about 145 miles north northwest of the city. Thus, the type locality is unknown.

Diagnosis. — A moderate-size species; males characterized by short mandibular projection; sides of aperture divided, forming moderately open pouches; telopodite long; acropodite short, about 1/4 of telopodite length, narrowly terminal, arising solely from inner prefemoral margin; prefemur with moderate number of hairs arranged continuously along inner surface, expanding distad into broad,



Figs. 102-107. *Eurymerodesmus simplex*. 102, projection of right mandible of holotype, lateral view. 103, aperture and gonopods *in situ* of holotype, ventral view. 104, left gonopod of holotype, lateral view. 105, the same, medial view. 106, left cyphopod of female from Evangeline Par., LA, medial view. 107, the same, anterior view. Scale line for fig. 103 = 1.00 mm. Line for other figs. = 0.30 mm for 102, and 0.50 mm for 104-107.

clavate shoulder on outer margin; cyphopod valves of females with subterminal marginal spur on medial valve, distal corners not produced; receptacle small, sides not curving around operculum.

Color in life. — Unknown.

Holotype. — Body highly fragmented, length unmeasurable, maximum width 4.2 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.2 mm, interantennal isthmus 0.9 mm. Antennae reaching back to mddle of 3rd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, and subantennal absent, frontal 1-1, genal 1-1, clypeal about 8-8, labral about 14-14. Process of mandibular stipes short and broad, apically indented (Fig. 102).

Collum extending below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-14, becoming progressively more acute beginning on segment 15.

5th sternum with low, rounded elevated areas between both leg pairs; 6th sternum with broad elevated areas between anterior legs and pair of long, conical, caudally directed projections between caudal legs, narrowly segregated in midline, longer than widths of adjacent coxae. Postgonopodal sterna with pair of broad knob-like processes between 9th legs, narrowly segregated in midline, apices angling anteriad, lengths subequal to widths of adjacent coxae; remaining sterna with variably elevated areas between both leg pairs on segments 8 and 9, caudal ones longer and tapering mediad, sterna becoming flatter and more plate-like with incomplete transverse impressions thereafter, with slight hair patches adjacent to coxae. 2nd coxa with broad anterior, and subacuminate posterior, lobes. Prefemoral lobes continuing through segment 9.

Gonopodal aperture (Fig. 103) subrectangular, with slight caudolateral pouches and broad anterior indentation, 1.9 mm wide and 0.8 mm long at maxima, outline of apparatus rectangular; anterior indentation short, broadly rounded; sides divided, slightly wider anteriad then narrowing, angling slightly mediad, and elevating beyond division point to caudolateral corner, division point located caudal to midlength, just before caudolateral corner, inner lateral margin very short, heading directly into inner caudolateral corner and then into inner caudal margin; outer caudal margin rising slightly to outer caudolateral corner, forming slight, open pouch with inner margin, rims slightly irregular; inner caudolateral corner indistinct; outer caudolateral corner rounded but sharp, nearly a right angle; inner caudal margin merging with outer margin just beyond caudolateral corner; outer caudal margin very short, extending from corner directly into inner margin, the two then continuing in slight bisinuate curve across midline, flush with metazonal surface; margins irregularly hirsute, with long hairs arising from anterior margin, thickest at anterolateral corners, with denser tufts of short hairs in pouches and a few short stiff hairs from caudal margin. Gonopods *in situ* (Fig. 103) with telopodites angling mediad and extending directly caudad, overlying each other in midline and projecting well beyond caudal margin, apices diverging over sternum between 9 legs. Gonopod structure as follows (Figs. 104-105): Telopodite terminating just before level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, leaning over coxa, expanding greatly beyond midlength into broad, clavate shoulder on outer margin, with two relatively sparse rows of continuous, but irregularly spaced hairs on inner margin to level of shoulder, culminating in a slight tuft, a distomedial tuft of about 12 hairs on shoulder at junction of acropodite, and one additional proximal hair on medial surface. Acropodite short and narrowly terminal, about 1/4 of telopodite length, arising from inner prefemoral margin, discontinuous with, and strongly demarcated from prefemur, much narrower than latter, bisinuate, apically blunt.

Female from Evangeline Par. — Approximate length 28.0 mm, maximum width 3.5 mm, W/L ratio 12.5%. Agreeing closely with holotype in somatic features, with following exceptions: Subantennal setae 1-1, genal 4-4. Mandibular stipes with short process, apically squared. Sterna relatively flat and unmodified, with variable, incomplete transverse impressions on all segments.

Cyphopodal aperture elliptical, sides and caudal margin elevated above metazonal surface. Cyphopods *in situ* with corners of valves protruding through aperture, open side facing anteriad. Valves (Figs. 106-107) moderately large and moderately hirsute, unequal, lateral larger than medial, oriented dorsoventrally in aperture, medial valve with subterminal marginal spur, distal corners not produced. Receptacle relatively small, glabrous, located dorsad to valves on caudal side, not curving partly around operculum. Latter moderate-size, tucked under open (anterior) side of valves.

Variation. — The gonopods of all males are nearly identical to those of the holotype. The aperture varies slightly in that it does not lean as far over the opening in some individuals, thus forming a shallower, more open concavity. In the male from Rapides Parish the caudal margin is distinctly elevated across the midline. Hairs arise irregularly all along the lateral rims and down the outer surfaces on

specimens from Evangeline and Rapides parishes. The lobes between the 9th legs are similar to those on the holotype in the Rapides Parish male and one from Evangeline Parish. The other Evangeline male possesses enormous subconical projections, much longer than the widths of the adjacent coxae, and they lean anteriad, thus displacing the apices of the telopodites. One lies between the lobes, and the other is pushed laterad over the coxa.

Ecology. — The Evangeline specimens were found under logs on a mixed pine-hardwood hillside.

Distribution. — Known definitely from the following two sites in central Louisiana (Figs. 54, 211).

LOUISIANA: *Rapides Par.,* Forest Hill, M, 11 October 1945, R. L. Wenzel (FMNH). *Evangeline Par.,* O.25 mi. S Rapides Par. line near Cocodrie Bayou, 2M, 3F, 1 February 1968, E. D. Keiser (FSCA).

Remarks. — The males from Evangeline and Rapides Parishes were tightly coiled and broke into several pieces upon handling, rendering length measurements impossible. The female measurement is only an approximation. However, *simplex* is generally a moderate-size species, smaller than *goodi* and *dubius,* but considerably larger than *varius.*

In proposing *Kewanius* for simplex Chamberlin (1938) did not officially form the new combination. This was done 20 years later by Chamberlin and Hoffman (1958), and remains the only formal publication of *K. simplex.*

This species is the fourth oldest in the genus, and it has never been illustrated. Causey (1963) restudied the types, claimed to find no differences warranting a new genus, and synonymized *Kewanius* with *Eurymerodesmus,* all without publishing a word of description or any illustrations. When I first saw the holotype I was surprised to see the discontinuous acropodite and clavate prefemur, since none of the previous works alluded to them. After analyzing *Eurymerodesmus* as a whole, I agree that *Kewanius* is a synonym, but it is amazing that Causey (1963) was so unimpressed by these characters that she did not even consider them worth mention. The discontinuity is so striking, that without studying all eurymerodesmids, I think one would have to give credence to Chamberlin's generic name.

Eurymerodesmus polkensis (Causey), new combination
Figs. 54, 108-115, 211

Paresmus polkensis Causey, 1952b:5, fig. 4. Chamberlin and Hoffman, 1958:83.

Type specimen. — Male holotype (AMNH) collected by N. B. Causey, 6 September 1950, 11 mi. N Mena, Polk Co., AR.

Diagnosis. — A large species; males characterized by large, broad mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating continuously, extending around caudolateral corners into moderately large, broadly rounded lobes on caudal margin; telopodite long; acropodite short, about 1/8 of telopodite length, narrowly terminal, arising from inner prefemoral margin; prefemur with many hairs arranged continuously along inner surface, not expanding distad, without detectable shoulder; females unknown.

Color in life. — Paranota red-orange; metaterga dark olive, prozonites darker, with red-orange "medial triangles" (Causey 1952b). None of the available specimens show evidence of color pattern, but from Causey's remarks, the species apparently displays middorsal spots instead of stripes.

Holotype. — Body highly fragmented, length unmeasureable, maximum width 6.6 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 3.0 mm, interantennal isthmus 1.1 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>5>6>3>4>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, subantennal, and genal absent, frontal 1-1, clypeal about 12-12, labral about 18-18. Process of mandibular stipes broad, heavily sclerotized, apically blunt (Fig. 108).

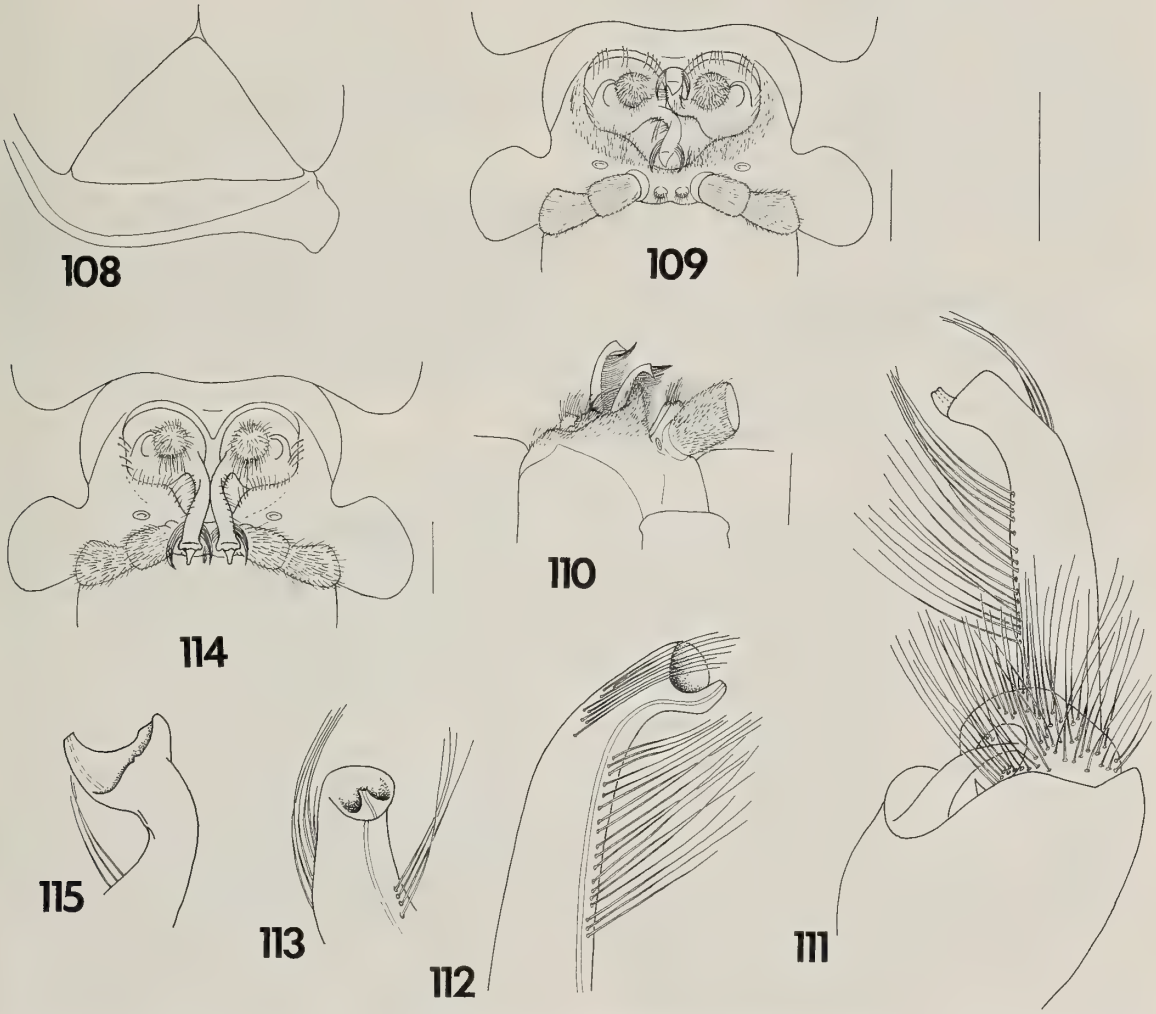
Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 8, blunt on 9-14, becoming progressively more acute caudally.

5th sternum with knob-like projections between both leg pairs, those between caudal (5th legs) larger and more widely segregated; 6th sternum with larger projections, those between caudal (7th) legs more widely separated. Postgonopodal sterna with short, knob-like processes between 9th legs; remaining sterna with lower elevations on segments 8-9, becoming progressively flatter and more sparsely hirsute caudally. 2nd coxa with strong subconical anterodistal, and short rounded posterior, lobes. Prefemoral lobes extending through segment 16.

Gonopodal aperture (Fig. 109, not this specimen) subrectangular, without caudolateral pouches, with strong anterior indentation, 2.7 mm wide and 1.0 mm long at maxima; anterior indentation long, triangular, acuminate; sides not divided, almost linear, curving very slightly caudomediad, elevating smoothly and continuously around caudolateral corner onto caudal margin, leaning only very slightly over opening, rims smooth; caudolateral corners rounded, obtuse; caudal margin continuing elevation of sides laterally, extending rapidly into moderately large, broadly rounded lobes (Fig. 110), tapering rapidly to metazonal surface and extending caudad in midline; margins densely hirsute, with tufts apically and along sides of anterior indentation, sporadic hairs along anterior margin, becoming progressively denser caudally along sides on rims and outer surfaces, densest on caudal lobes,

narrowing into a row along caudal midline. Gonopods *in situ* (Fig. 114, not this specimen) with telopodites abutting or overlying each other in midline of aperture, diverging, extending over caudal margin, and terminating over sternum between 9th legs. Gonopod structure as follows (Figs. 111-113): Telopodite terminating before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, sublinear and of nearly uniform width for most of length, narrowing distad and curving dorsad, with slight cavity on apical margin, with two rows of continuous, regularly spaced hairs along inner surface and distomedial tuft of about 10 hairs. Acropodite short and narrowly terminal, about 1/8 of telopodite length, arising from inner distal margin of prefemur, discontinuous with, and sharply demarcated from latter, curving slightly ventrad, apically blunt.

Variation. — The male from Scott County measures 39.4 mm in length, 6.2 mm in width, W/L ratio 15.7%. The lobes on the caudal margin of the aperture appear slightly smaller than those of the type, and the caudal margin extends farther caudad in the midline. The left gonopod was displaced and directed ventrad rather than caudad (Fig. 109). The unbroken specimen from Montgomery County measures 33.7 mm long, 5.4 mm wide, W/L ratio 16.0%. The lateral margins of the aperture are more strongly elevated, and the lobes are distinctly higher but markedly less hirsute. On the gonopods the prefemur is bent more strongly distad, and the acropodite extends around the distal extremity of the prefemur and is expanded and cupped to form a definite terminal calyx (Fig. 115) with irregular margin.



Figs. 108-115. *Eurymerodesmus polkensis.* 108, projection of right mandible of holotype, lateral view. 109, aperture and gonopods *in situ* of male from Scott Co., AR, ventral view. 110, the same, lateral view. 111, left gonopod of holotype, lateral view. 112, telopodite of the same, medial view. 113, apex of the same, ventral view. 114, aperture and gonopods *in situ* of male from Montgomery Co., AR, ventral view. 115, apex of telopodite of left gonopod of the same, lateral view. Scale lines for figs. 109-110 and 114 = 1.00 mm. Line for other figs. = 0.30 mm for 108 and 111, 0.40 mm for 112, and 0.50 mm for 113 and 115.

Ecology. — Notations on the vial labels indicate that the male from Scott County was taken on a wooded hillside; those from Montgomery County were discovered in a "pig dung trap."

Distribution. — Known only from three adjacent counties in western Arkansas (Figs. 54, 211). Specimens were examined as follows:

ARKANSAS: *Scott Co.,* 4 mi. W Y City, M, 24 October 1963, L. Hubricht (RLH). *Polk Co.,* 11 mi. N Mena, M, 6 September 1950, N. B. Causey (AMNH) TYPE LOCALITY. *Montgomery Co.,* Muddy Cr. Wildlife Management Area, along US hwy. 270, 5.2 mi. W Pencil Bluff, 2M, 6-8 March 1977, R. E. Woodruff (FSCA).

Remarks. — *Eurymerodesmus polkensis* is placed in the *Kewanius* lineage, *simplex* group, because of the discontinuous prefemora, but it could equally well go in the *birdi* lineage because of the undivided aperture sides, the absence of pouches, and the distinct lobes on the caudal margin. By combining the aperture of *birdi* with the *simplex/-varius* gonopod, *polkensis* proves that the undivided/lobed-divided/pouch aperture extremes are congeneric.

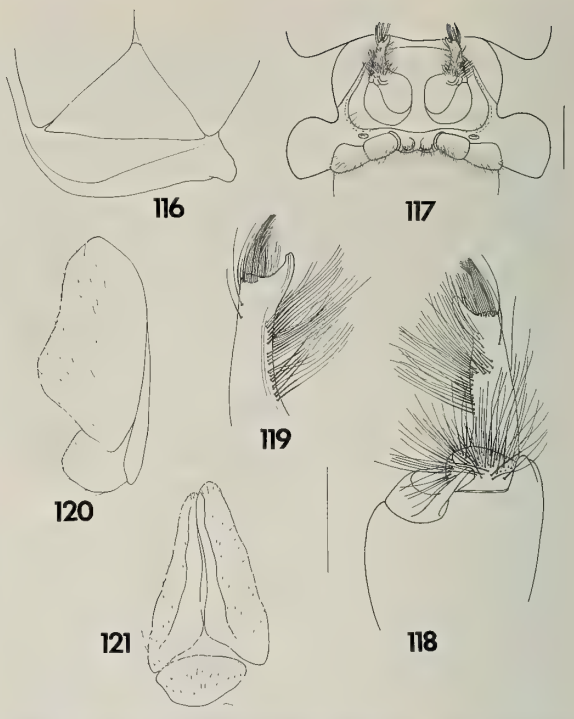
Eurymerodesmus caesariatus, new species
Figs. 54, 116-121

Type specimens. — Male holotype and one female and one juvenile paratype (FSCA) collected by N. B. Causey, 23 December 1953, 7 mi. N Meadville, Franklin Co., MS.

Diagnosis. — A moderate-size species; males characterized by moderately long mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating slightly, continuing around caudolateral corner, and tapering rapidly to metazonal surface a short distance onto caudal margin; telopodite short, extending directly ventrad not caudad, wholly enclosed within aperture; acropodite short, about 1/4 of telopodite length, arising solely from inner prefemoral margin; prefemur not expanding distad, without detectable shoulder, with many hairs arranged continuously along inner surface and dense terminal corona lying parallel to acropodite; cyphopod valves of females moderately large, distal corners slightly elongate; receptacle narrow, sides not curving around operculum.

Color in life. — Unknown. The blanched types lack any trace of either color or pattern.

Holotype. — Length 27.0 mm, maximum width 4.2 mm, W/L ratio 15.6%.



Figs. 116-121. *Eurymerodesmus caesariatus.* 116, projection of right mandible of holotype, lateral view. 117, aperture and gonopods *in situ* of holotype, ventral view. 118, left gonopod of holotype, lateral view. 119, telopodite of the same, medial view. 120, left cyphopod of female paratype, medial view. 121, the same, anterior view. Scale line for fig. 117 = 1.00 mm. Line for other figs. = 0.30 mm for 116, 0.40 mm for 118 and 120-121, and 0.50 mm for 119.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.4 mm, interantennal isthmus 0.6 mm. Antennae reaching back to just beyond caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, subantennal 1-1, clypeal about 8-8, labral about 14-14. Process of mandibular stipes moderately long, apically blunt (Fig. 116).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 10, blunt on 11-14, becoming progressively more acute caudally.

5th sternum with short, subequal, knob-like projections between leg pairs, those between caudal (5th) legs more widely separated; 6th sternum with similar knobs between anterior legs and broad, flattened, elevated areas between caudal legs. Postgonopodal sterna with low, densely hirsute, knob-like processes between 9th legs; remaining sterna with hirsute elevated areas on segments 8-10, becoming progressively flatter, more plate-like, and less hirsute caudally, caudalmost sterna glabrous or nearly so. 2nd coxa with short, conical anterior, and minute rounded caudal, lobes. Prefemoral lobes extending through legs on segment 10.

Gonopodal aperture (Fig. 117) broadly trapezoidal, without caudolateral pouches and anterior indentation, 1.5 mm wide and 0.8 mm long at maxima; anterior margin without trace of indentation; sides not divided, angling caudolaterad, elevating imperceptibly

tibly to caudolateral corner, not leaning over opening, rims smooth; caudolateral corner broadly rounded; caudal margin continuing elevation of sides laterally, tapering rapidly to metazonal surface, extending slightly caudad in midline; margins almost glabrous, with only very few hairs on caudolateral corners. Gonopods *in situ* (Fig. 117) with telopodites extending nearly directly ventrad, in parallel arrangement, completely enclosed by opening, oriented vertically and perpendicular to body axis, not extending caudad. Gonopod structure as follows (Figs. 118-119): Telopodite relatively short, terminating well before level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, configuration linear, widening beyond midlength then narrowing distad, with two dense rows of continuous, regularly spaced hairs along inner margin, additional hairs between rows, and dense terminal marginal tuft of 16 or so very broad hairs lying parallel to and obscuring acropodite, and forming corona. Acropodite short and narrowly terminal, about 1/4 of telopodite length, obscured by terminal prefemoral hairs, arising from inner margin of distal extremity of prefemur, discontinuous with, and sharply demarcated from, latter, curving slightly ventrad, apically rounded.

Female paratype. — Body highly fragmented, length unmeasurable, maximum width 3.9 mm. Somatic features agreeing essentially with holotype, with following exceptions: Process of mandibular stipes minute, rounded, barely projecting from stipital surface. 3rd sternum with two minute, hirsute lobes, remaining sterna flat and essentially glabrous.

Cyphopodal aperture subrectangular, sides elevated above metazonal surface. Cyphopods *in situ* with corners of valves protruding through aperture, valves oriented along body axis. Valves (Figs. 120-121) relatively large, subequal, distal corners slightly prolonged and rounded, moderately hirsute. Receptacle narrow, located on caudal surface of valves, closely adhering to latter, sides not curving partly around operculum. Latter comparatively large, clearly visible under free, anterodorsal corner of valves.

Ecology. — Unknown.

Distribution. — Known only from the type locality (Fig. 54).

Remarks. — The terminal prefemoral hairs are packed so tightly that they superficially resemble a sclerotized lamella; at first glance there appeared to be a terminal clayx. They form a semicircular corona and I think are homologous to the distomedial tuft on other species, which is situated more on the medial surface a short distance from the end of the prefemur.

In general configuration, the telopodite of *caesariatus* is closest to that of *polkensis*. However, *caesariatus* occurs some 280 miles southeast of *polkensis*, so the intervening part of Arkansas and Louisiana probably contains other forms with narrowly terminal acropodites.

Eurymerodesmus paroicus (Chamberlin), new combination
Figs. 54, 122-125, 211

Paresmus paroicus Chamberlin, 1942a:7, pl. 2, figs. 18-19. Chamberlin and Hoffman, 1958:82.

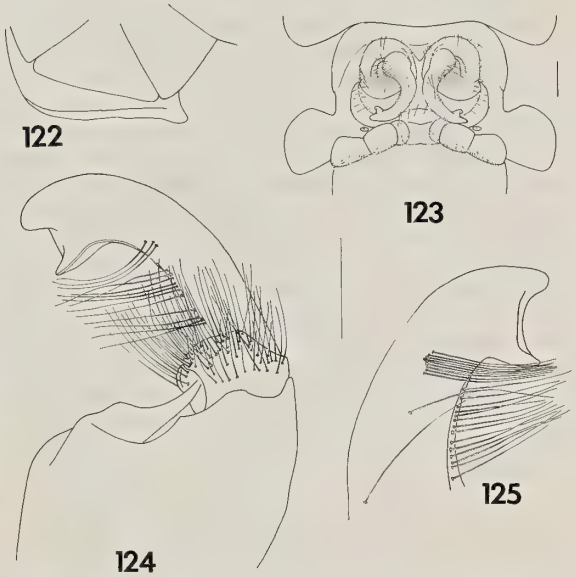
Type specimen. — Male neotype and one additional male (FSCA) collected by W. J. Harmon, December 1954, 900 S. Farmerville St., Ruston, Lincoln Par., LA. This site is around 5-6 miles north of the type locality, 1.5 mi. N Clay, at the border of Lincoln and Jackson Parishes. The type vial, containing the original label, is at the NMNH, but it contains four males of *Pseudopolydesmus pinetorum* (Bollman) and not even a loose eurymerodesmid segment. Thus the type series, containing the holotype and an unknown number of paratypes, is lost.

Diagnosis. — A moderate to large species; males characterized by short mandibular projection; sides of aperture divided, forming shallow open pouches; telopodite long; acropodite short, about 1/8 as long as prefemur arising subterminally from inner prefemoral margin; prefemur very long and very broad, comprising entire length of telopodite, with rounded, glabrous, distal lobe overhanging and extending beyond level of acropodite and with modest number of hairs arranged continuously along inner margin to near base of acropodite, inner surface smooth, not excavated; females unknown.

Color in life. — Unknown.

Neotype. — Body highly fragmented, length unmeasurable, maximum width 4.0 mm.

Somatic features similar to *hispidipes*, with following exceptions:



Figs. 122-125. *Eurymerodesmus paroicus*. 122, projection of right mandible of neotype, lateral view. 123, aperture and gonopods *in situ* of neotype, ventral view. 124, left gonopod of the same, lateral view. 125, telopodite of the same, medial view. Scale line for fig. 123 = 1.00 mm. Line for other figs. = 0.13 mm for 122, 0.40 mm for 124, and 0.50 mm for 125.

Width across genal apices 2.6 mm, interantennal isthmus 0.9 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>4>3>5>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial 1-1, interantennal and frontal absent, subantennal 1-1, genal 4-4, clypeal about 10-10, labral about 13-13. Mandibular stipes with short, narrowly rounded projection (Fig. 122).

Collum not extending below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners blunt on anterior segments, becoming progressively prolonged and acute posteriorly.

Sternum of segment 5 with broad, flattened, elevated areas between both pairs of coxae, caudal elevations (between 5th legs) higher and more segregated in midline; 6th sternum with elevations stronger, more rounded, and more densely hirsute, caudal ones (between 7th legs) higher. Postgonopodal sterna with low, widely segregated lobes between 9th legs; remaining sterna becoming progressively flatter and more plate-like posteriorly, with slight hirsute lobes adjacent to coxae on segments 8 and 9, tapering into hirsute patches on 10-11, becoming less dense caudally, with variably impressed transverse grooves originating between leg pairs. 2nd coxa with strong, conical anterior, and shorter rounded posterior, lobes. Prefemoral lobes extending through anterior legs of segment 12.

Gonopodal aperture (Fig. 123) broadly rectangular, with narrow, open caudolateral pouches and strong anterior indentation, 2.8 mm wide and 1.7 mm long at maxima, outline of apparatus subtrapezoidal; anterior indentation long, triangular apically acute; sides divided, curving slightly mediad, rising to division point caudal to midlength and leaning imperceptibly over opening, inner lateral margin plunging directly dorsad into opening then curving broadly into inner caudolateral corner, outer lateral margin upright, well separated from inner, flaring caudolaterad and dropping slightly to caudolateral corner, forming shallow open pouch with inner margin, rims slightly irregular; inner caudolateral corner broad, rounded, visible deep inside opening; outer caudolateral corner broadly rounded but approximately 90°; inner caudal margin curving smoothly across midline well inside opening, generally invisible; outer caudal margin dropping slightly from caudolateral corner to metazonal surface, running along anterior surfaces of coxal condyles, extending slightly caudad in midline; margins moderately hirsute with long hairs arising sporadically from rims and overhanging opening, slightly denser on anterior indentation, much denser at division points on sides, with relatively sparse growths from pouches evenly dispersed; caudal margin with a few widely separated hairs. Gonopods *in situ* (Fig. 123) with telopodites diverging and angling caudolaterad over inner caudal margin of aperture, acropodites directed dorsad. Gonopod structure as follows (Figs. 124-125): Telopodite terminating at level of distal extremities of hairs. Prefemur very long and broad, comprising entire length of telopodite, distal third glabrous, curving gently and leaning over coxa, curve increasing distad, terminating in broadly rounded lobe overhanging and extending beyond level of acropodite, of nearly subequal width throughout, narrowing slightly distad, with ridge along inner surface demarcating prostatic groove, with two rows of subcontinuous hairs along inner margin terminating proximal to origin of acropodite, distolateral tuft of 3 hairs, dense distomedial tuft of about 9-12 hairs, and 2 long proximal hairs on medial surface. Acropodite short, about 1/8 as long as prefemur, profile subtriangular, arising subterminally on inner surface of prefemur, sides narrowing rapidly to subacuminate tip, directed dorsad.

Variation. — All males of *paroicus* are fragmented beyond the point where they can be reassembled for measurements. The only noticeable variation is slight differences in the alignment of the lateral aperture margins. They are linear in the neotype, angled slightly caudolaterad in another male, and bowed slightly in the others. The last two conditions result in slightly larger pouches.

Ecology. — According to Chamberlin (1942a), the type series was encountered under logs.

Distribution. — Known only from Lincoln Parish, Louisiana (Figs. 54, 211). Specimens were examined as follows:

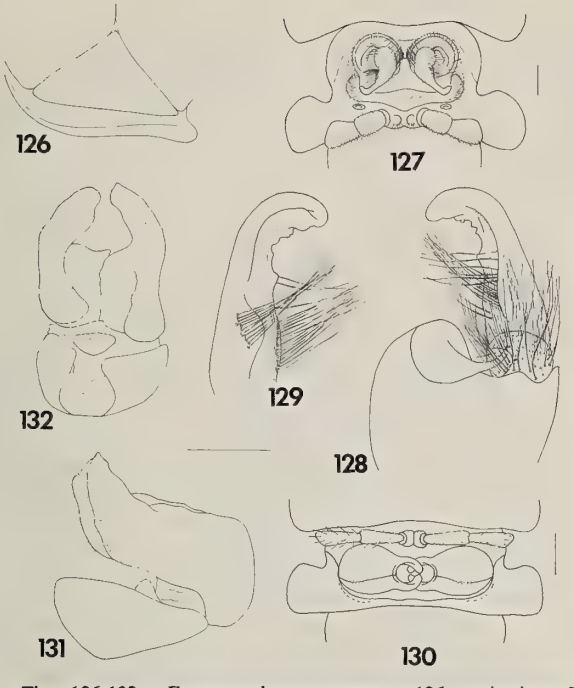
LOUISIANA: *Lincoln Par.,* Ruston, 900 S. Farmerville St., 2M, December 1954, W. J. Harmon (FSCA) NEOTYPE; and unknown location in Ruston, 2M, October and November 1951, collectors unknown (FSCA).

Remarks. — The gonopod of *paroicus* is one step removed from the condition in *polkensis.* If the apex of the latter's prefemur were swollen and extended slightly beyond the acropodite, the two would be practically interchangeable except for the slightly greater thickness of *paroicus.* However, the apertures are entirely different. That of *paroicus* has divided lateral margins and caudolateral pouches, whereas that of *polkensis* displays undivided sides and caudal lobes.

Eurymerodesmus crassatus, new species
Figs. 54, 126-132, 211

Type specimens. — Male holotype and 6 male and 2 female paratypes (FSCA) collected by L. D. Wilson, 24 March 1966, off old US highway 165, 2.6 mi. S Georgetown, Grant Par., LA. One male and one female paratype deposited in NCSM.

Diagnosis. — A moderate to large species; males characterized by short mandibular projection; sides of aperture divided, with open caudolateral pouches; telopodite long; acropodite minute, no more than 1/10 as long as prefemur, nubbinlike, arising subterminally from inner prefemoral margin; prefemur very long and very broad, comprising entire length of telopodite, with broad distal lobe overhanging and extending well beyond level of acropodite, with modest number of hairs arranged continuously along inner margin to near base of acropodite, inner surface emarginate; cyphopod valves of females with bowed projections from distal corners, apices touching or nearly so; receptacle moderate-size, sides curved partly around operculum.



Figs. 126-132. *Eurymerodesmus crassatus.* 126, projection of right mandible of holotype, lateral view. 127, aperture and gonopods *in situ* of paratype, ventral view. 128, left gonopod of the same, lateral view. 129, telopodite of the same, medial view. 130, cyphopods *in situ,* ventral view of female paratype. 131, left cyphopod of the same, caudal view. 132, the same, medial view. Scale lines for figs. 127 and 130 = 1.00 mm. Line for other figs. = 0.35 mm for 126 and 131, 0.40 mm for 128, and 0.50 mm for 129 and 132.

Color in life. — Unknown. The specimens are uniformly tawny after 23 years in alcohol and exhibit no trace of either color or pattern.

Holotype. — Length 25.0 mm, maximum width 4.1 mm, W/L ratio 16.4%.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.7 mm, interantennal isthmus 0.8 mm. Antennae reaching back to middle of 3rd tergite, relative lengths of antennomeres 2>3>5>4>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 9-9, labral about 16-16. Process of mandibular stipes short, broadly rounded (Fig. 126).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, somewhat interrupting slope of dorsum, peritremata flattened; posterior corners rounded through segment 3, blunt on 4-10, becoming progressively more acute caudally.

5th sternum with narrowly rounded, slightly elevated areas between both coxae; 6th sternum with broader, higher, flattened areas between coxae. Postgonopodal sterna with low, rounded elevations between 9th coxae; remaining sterna becoming progressively flatter and more plate-like caudally, with sparsely hirsute patches adjacent to coxae. 2nd coxa with moderately large, broadly rounded anterior lobe and slightly shorter, subacute caudal one. Prefemoral lobes present on all but ultimate two leg pairs.

Gonopodal aperture (Fig. 127, not this specimen) broadly ovoid, with open caudolateral pouches and strong anterior indentation, 2.4 mm wide and 1.1 mm long at maxima, outline of apparatus broadly trapezoidal; anterior indentation long, triangular; sides curving gently mediad and leaning progressively over opening, rising to division point caudal to midlength, inner lateral margin exposed, extending nearly directly dorsad, curving strongly into inner caudolateral corner, outer lateral margin curling sharply dorsolaterad, not obscuring inner margin, dropping to outer caudolateral corner, forming shallow, open pouch with inner margin; inner caudolateral corner comparatively sharp, approximately a right angle; outer caudolateral corner broadly rounded; inner caudal margin flush with metazonal surface, extending slightly inward into opening; outer caudal margin dropping to metazonal surface shortly after outer caudolateral corner, extending caudad in midline; margins moderately hirsute, with tufts of 8 or so hairs on sides of anterior indentation, regularly spaced hairs along rest of anterior margin and sides to division point, moderate tufts in pouches, and scattered hairs between caudal margins. Gonopods *in situ* (Fig. 127, not this specimen) with telopodites widely separated and diverging, extending caudolaterad over inner caudal margin, apices curving sublaterad. Gonopod structure as follows (Figs. 128-129): Telopodite essentially terminating at level of distal extremities of hairs. Prefemur very long, comprising entire length of telopodite, distal third glabrous, extending linearly for most of length, curving broadly distad and overhanging and extending well beyond level of acropodite in broadly rounded terminal lobe, very broad basally, widening into broad shoulder on medial surface near midlength, narrowing thereafter and tapering to broadly rounded tip, inner surface emarginate, with row of subcontinuous hairs on inner surface extending to just beyond shoulders and dense distal tufts of 15 or so hairs on lateral and medial surfaces of shoulders, latter located slightly distal to former. Acropodite minute and indistinct, a short, nubbinlike extension of inner surface of prefemur near base of distal curvature, no more than 1/10 as long as prefemur.

Female paratype. — Length 23.2 mm, maximum width 4.0 mm, W/L ratio 17.2%. Agreeing closely with males in structural details, with following exceptions: Process of mandibular stipes short, subacute.

Cyphopodal aperture broadly ovoid, sides strongly elevated above metazonal surface. Cyphopods *in situ* with edges of valves and projections visible in aperture (Fig. 130). Valves (Figs. 131-132) large, subequal, oriented transversely in aperture, leaning over receptacle, distal corners extending into broad, digitiform lobes, curving towards each other with apices touching or nearly so, with scattered hairs on projections. Receptacle relatively large, glabrous, located directly beneath valves, sides cupped partly around operculum. Latter small, hidden beneath, and obscured by, valves.

Male paratypes. — The male paratypes agree with the holotype in all particulars.

Ecology. — The types were taken at an old mill site, but the habitat is not indicated on the vial label.

Distribution. — Known only from the type locality.

Remarks. — This species is similar to *paroicus,* and future collecting in the gap of around 40 miles may show them to connect and be geographic races.

The apertures are very close, and the major differences involve the much shorter acropodite and irregular inner margin of *crassatus*.

The female is suspiciously similar to those of *angularis* in the valvular projections and may actually be referrable to this species, occuring only two counties to the east. However, the position of the valves directly above the receptacle (Fig. 131) is unique, so it may be conspecific with the males.

Eurymerodesmus pulaski (Causey), new combination
Figs. 54, 133-140, 211

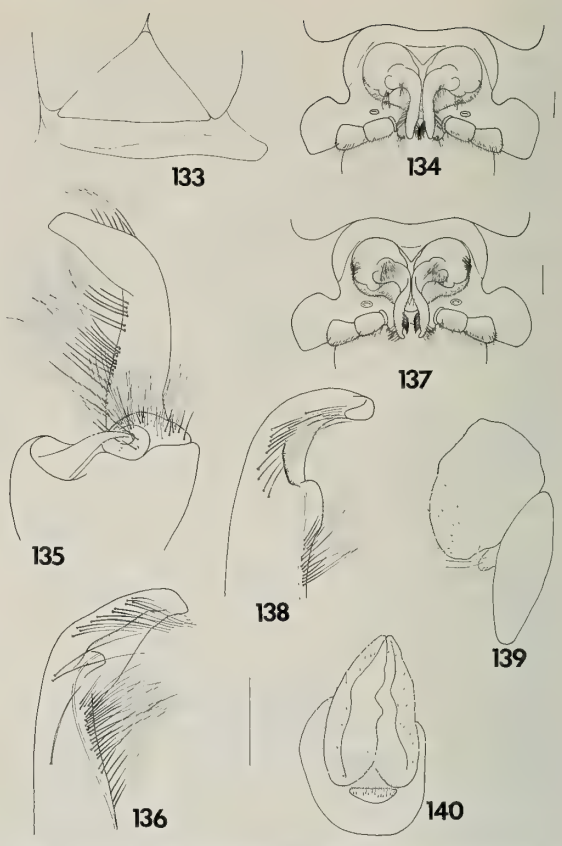
Leptodesmus hispidipes: Bollman, 1888a:2, in part.
Paresmus pulaski Causey, 1950a:271-272, fig. 9; 1952b:4-5. Chamberlin and Hoffman, 1958:83.

Type specimen. — Male neotype, two additional males, and one female (NMNH) collected by C. H. Bollman, on an unknown date in the 1880's before 1888, at Little Rock, Pulaski Co., AR. The type locality, 3 mi. S Sweet Home, is on the southern periphery of Little Rock, and the type series consisted of two males collected in 1949. The holotype, reportedly at the ANSP (Causey 1950a, Chamberlin and Hoffman 1958), and the paratype, retained in Causey's private collection (Causey 1950a), now at the FSCA, are lost.

Diagnosis. — A moderate to large species; males characterized by long mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating slightly, curving around caudolateral corners, with suggestion of lobe on caudal margin; telopodite long, acropodite minute, less than 1/10 as long as prefemur, a blunt spur arising subterminally from inner prefemoral margin and situated in cavity in latter; prefemur very long and broad, comprising entire length of telopodite, expanding at level of acropodite into hood overhanging and shielding latter, broadly sublinear or distally uncinate, with cavity on inner margin and many hairs arranged continuously along inner surface; cyphopod valves of females not modified, distal corners not extended; receptacle moderately large, sides expanding but not curving around operculum.

Color in life. — Paranota orange; metaterga dark olive, prozonites darker, with orange stripes along caudal margins connecting paranotal markings, expanding slightly mediad; collum with stripes on anterior and posterior margins (Causey 1950a).

Neotype. — Body highly fragmented, length unmeasurable, maximum width 5.2 mm.



Figs. 133-140. *Eurymerodesmus pulaski.* 133, projection of right mandible of neotype, lateral view. 134, aperture and gonopods *in situ* of neotype, ventral view. 135, left gonopod of the same, lateral view. 136, telopodite of the same, medial view. 137, aperture and gonopods *in situ* of male from Pulaski Co., AR, ventral view. 138, apex of telopodite of left gonopod of the same, medial view. 139, left cyphopod of female from Pulaski Co., lateral view. 140, the same, medial view. Scale lines for figs. 134 and 137 = 1.00 mm. Line for other figs. = 0.25 mm for 133, 0.37 mm for 135, 0.40 mm for 139-140, and 0.50 mm for 136 and 138.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 3.2 mm, interantennal isthmus 0.8 mm. Antennae reaching back to middle of 3rd tergite, relative length of antennomeres 2>3>4>6>5>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, subantennal, frontal, and genal absent, clypeal about 10-10, labral about 15-15. Process of mandibular stipes long, subconical, tapering to blunt tip (Fig. 133).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 5, blunt on 6-11, becoming progressively more acute posteriorly. 2nd coxa with moderate-size subconical anterior lobe, caudal lobe only slightly smaller. Prefemoral lobes extending through segment 10.

Gonopodal aperture (Fig. 134) broadly ovoid, without caudolateral pouches, with strong anterior indentation, 2.7 mm wide and 1.0 mm long at maxima; anterior indentation long, triangular, acute; sides not divided, curving gently mediad, rising very slightly to caudolateral corner, not leaning over opening, rims

smooth; caudolateral corner broadly rounded, slightly elevated, forming a slightly obtuse angle; caudal margin rising slightly into suggestion of lobe then tapering to metazonal surface, extending caudad in midline; anterior margin glabrous, hairs beginning at midlength of sides and continuing onto caudal margin, regularly spaced. Gonopods *in situ* (Fig. 134) with telopodites extending caudad in parallel arrangement, extending well beyond aperture, overhanging sternum between 9th legs, apices directed dorsad. Gonopod structure as follows (Figs. 135-136): Telopodite terminating near level of distal extremities of hairs. Prefemur long, comprising entire length of telopodite, configuration slightly bisinuate, bending strongly dorsad distally, narrow basally, expanding beyond midlength into concave hood shielding acropodite, narrowing distad, apically blunt, with cavity on inner surface of hood, two rows of continuous, subregularly spaced hairs on inner surface to near distal bend, tuft of around 10 hairs on inner surface just before distal bend, distomedial tuft of around 10 hairs on hood, and 4 or so scattered hairs proximally on medial margin. Acropodite minute, a blunt subtriangular spur located subterminally in cavity on undersurface of hood at level of distal bend, partly shielded by sides of hood.

Female from Pulaski Co. — Body highly fragmented, length unmeasurable, maximum width about 4.5 mm. Process of mandibular stipes short, truncate. Other somatic features unknown because of great fragmentation and mixture of male and female segments in sample; impossible to reliably segregate segments by sex.

Cyphopodal aperture ovoid, sides flush with metazonal surface. Cyphopods *in situ* with edges of valves visible in aperture. Valves (Figs. 139-140) moderate-size, subequal, oriented transversely in aperture, medial (open) side densely hirsute, corners not extended. Receptacle moderately large, glabrous, located laterad at bases of valves, sides expanding beyond latter but not cupped around operculum. Latter small, located under free (open) end of valves.

Variation. — The neotype was chosen because it is the only available male matching Causey's illustration (1950a, fig. 9) of the holotype; it may have come from the same general area in south Little Rock. The NMNH sample contains fragments of two different males that may occur sympatrically in Little Rock. One exhibits sufficient gonopodal similarities to the neotype to be considered conspecific, but the other is so different as to require another binomial, and is therefore described in the ensuing account. The female in this sample may well be assignable to the following species, the other samples of which contain only males. There being no way this can be determined at present, I arbitrarily assign it to *pulaski*.

The acropodite of the variant is rudimentary, a thickened boss barely elevated above the prefemoral surface (Fig. 138). The cavity on the undersurface of the prefemur is very deep; the hood curves well over the acropodite as in the neotype; and the tip curls mediad to a subacuminate tip. The aperture configuration is the same, but the elevations on the caudal margin are higher, more distinctly lobe-like, and more densely hirsute (Fig. 137).

Ecology. — The type series was taken in an oak-pine association (Causey 1950a).

Distribution. — Known only from Pulaski County, Arkansas (Fig. 54, 211). The neotype and the associated males are the only available specimens.

Remarks. — Because of the high fragmentation of the Bollman and Hutcherson samples, it is impossible to determine which segment is which and thus to report the conditions of the sterna.

The neotype is one of Bollman's original samples and the label is in his handwriting. Consequently, this is probably one of the species he (1888a) identified as *"Leptodesmus hispidipes"* and stated was very common throughout Arkansas.

Pulaski County, and the area around Little Rock specifically, need to be meticulously sampled, since at least three forms occur there. At this writing I cannot determine if they are sympatric or parapatric; Bollman could well have combined samples from distant sites in the county under the general heading of Little Rock.

Eurymerodesmus serratus, new species
Figs. 54, 141-146, 211

Leptodesmus hispidipes: Bollman, 1888a:2, in part.

Type specimen. — Male holotype (FSCA) collected by "Coffee," 11 October 1955, at Cato, Pulaski Co., AR. Male paratype (FSCA) collected G. B. Edwards, 4 November 1978, ca. 10 mi. SE Gainesville, along FL hwy. 325, 4 mi. S jct. FL hwy. 20, Alachua Co., FL.

Diagnosis. — A moderate to large species; males characterized by long mandibular projection; sides of aperture not divided, without caudolateral pouches, rising gradually to short lobe at caudolateral corners, caudal margin descending rapidly to metazonal surface; telopodite long; acropodite minute, less than 1/10 as long as pefemur, arising subterminally from inner prefemoral margin at base of expansion, situated in cavity in latter; prefemur very long, comprising entire length of telopodite, expanding greatly at level of acropodite into short, broad hood overhanging and shielding latter, margins of hood irregularly serrate to jagged, with cavity on inner margin and many hairs arranged continuously along inner surface; females unknown.

Color in life. — Unknown. Though faded, the Florida male shows evidence of stripes along the caudal metatergal margins connecting with the paranotal markings and expanding in the midline; the collum is striped along both margins.

Holotype. — Body highly fragmented, length unmeasurable, maximum width 5.1 mm.

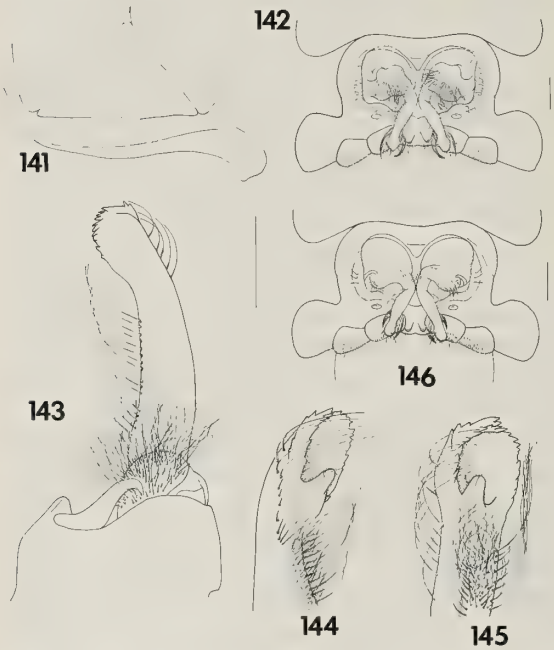
Somatic features similar to *hispidipes,* with following exceptions:

Head partly decomposed, facial characters obtained from paratype.

Collum not extending below ends of following tergite. Paranota moderately depressed, partly continuing slope of dorsum; posterior corners rounded through segment 10, blunt on 11-12, becoming progressively more acute caudally.

5th sternum with short, narrowly segregated, knob-like processes between anterior (4th) legs and broader, higher, widely separated ones between 6th legs; 5th sternum with subsimilar knob-like projections between both leg pairs, those between caudal (7th) legs slightly higher. Postgonopodal sterna with strong, subconical, widely separated lobes subtending coxae of 9th legs, only slightly shorter than widths of latter; remaining sterna with short, broad lobes between both legs on segment 8, becoming progressively flatter posteriorly, with modest hair patches beside legs on all segments. 2nd coxa with strong subconical anterior, and slightly shorter posterior lobes. Prefemoral lobes extending through segment 15.

Gonopodal aperture (Fig. 142) ovoid, without caudolateral pouches, with strong anterior indentation, 2.1 mm wide and 1.1 mm long at maxima; anterior indentation relatively long, triangular, apically acute; sides not divided, angling slightly mediad, rising gradually and continuously to short lobe at caudolateral corner, rims smooth; caudolateral corner broad, indistinct; caudal margin continuous with lobe at caudolateral corner, dropping rapidly a short distance from latter to metazonal surface, curving across midline and extending slightly caudad; margins irregularly hirsute with scattered hairs on anterior margin, none on indentation, relatively dense hairs arising on outer surfaces of sides and extending rather continuously to end of elevation on caudal margin, lobes without denser hairs. Gonopods *in situ* (Fig. 142) with bases of telopodites touching or nearly so in midline, diverging and extending well beyond caudal margin of aperture, overhanging 9th coxae, terminating over caudal margin of 7th segment, apices directed dorsad. Gonopod structure as as follows (Figs. 142-145): Telopodite terminating at level of distal extremities of hairs. Prefemur very long, comprising entire length of telopodite, apically glabrous, configuration slightly curved with lengthy linear section in middle, apex bending more strongly dorsad, narrow basally, expanding markedly at midlength, narrowing slightly at distal bend, then expanding in perpendicular plane into short, broad, marginally serrated hood, inner surface strongly concave, with two rows of continuous, regularly spaced hairs on inner and lateral margins extending to just short of distal bend and level of acropodite, distomedial tuft of 6 or so hairs extending to midlength of hood, and one or two more proximal hairs medially. Acropodite a short, blunt spur on inner surface of prefemur, shielded ventrally but not surrounded by hood, directed outward or dorsad.



Figs. 141-146. *Eurymerodesmus serratus.* 141, projection of right mandible of paratype, lateral view. 142, aperture and gonopods *in situ* of holotype, ventral view. 143, left gonopod of the same, lateral view. 144, telopodite of the same, medial view. 145, the same, dorsal view. 146, aperture and gonopods *in situ* of male from Alachua Co., FL, ventral view. Scale lines for figs. 142 and 146 = 1.00 mm. Line for other figs. = 0.25 mm for 141, 0.30 mm for 143, and 0.50 mm for 144-145.

Male paratype. — Fragmented, unmeasurable. Width across genal apices 3.9 mm, interantennal isthmus 1.1 mm. Antennae reaching back beyond caudal margin of 3rd tergite, relative lengths of antennomeres 2>6>4>5>3>1>7. Genae without impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 11-11, labral about 21-21. Process of mandibular stipes relatively long, angling slightly caudad, apically rounded (Fig. 141).

The male paratype agrees closely with the holotype, which is remarkable considering the 700 mile gap between them. The sternal projections on segments 4 and 5 are perhaps slightly longer, but otherwise there are no differences in somatic features. The aperture is considerably less hirsute, but its configuration is very similar to that of the holotype (Fig. 146). The elevations begin more suddenly a short distance back from the anterolateral corner, plateau, and continue around the caudolateral corner into a less distinct lobe, located more on the caudal margin. Aside from a slightly different degree of serration on the hood, the gonopods are virtually identical.

Variation. — The male from Little Rock agrees closely with the holotype in all particulars.

Ecology. — There are no indications of habitat on the vial labels with the Arkansas males. That from Florida was found on top of litter at the base of a small water oak in a wooded transition zone between slash pine and water oak.

Distribution. — Known from two widely separated sites, about 700 miles apart, in central Arkansas and northern Florida (Fig. 54). It is unknown whether these reflect truly allopatric populations or if the hiatus contains numerous additional populations, such that the range is reasonably continuous. Specimens were examined as follows:

ARKANSAS: *Pulaski Co.,* Cato, just S of Faulkner Co. line, M, 11 October 1955, Coffee (FSCA) TYPE LOCALITY; and Little Rock, M, 1880's, Hutcherson (NMNH).

FLORIDA: *Alachua Co.*, 10 mi. SE Gainesville, along FL hwy. 325, 4 mi. S jct. FL hwy. 20, M, 4 November 1978, G. B. Edwards (FSCA).

Remarks. — The three males of this species are so highly fragmented that length measurements would be meaningless. However, the animals can be characterized as "moderately-large," i.e. smaller than such species as *goodi* and *dubius,* but larger than other intermediate-size species like *hisipdipes.* The male from Little Rock is only a partial specimen, consisting of segments 6-9, and was mixed in the same vial with the neotype and two fragmented male variants of *pulaski.* Since this sample was labeled *"Leptodesmus hispidipes"* by Bollman in his handwriting, *serratus* probably constitutes part of the basis for his published record (1888a). Included in this vial is part of a female, which I characterized in the *pulaski* account but which may be referrable to *serratus.* The bulk of the NMNH sample consists of mixed segments that cannot be segregated either by sex or species. The holotype and paratype were preserved intact, but they were so rigid and tightly coiled that they shattered when I tried to open them for examination, determination, and measurement.

The configuration of the telopodite of *serratus* is remarkably similar to those of the xystodesmids *Sigmoria (Cheiropus) planca* (Loomis) and *S. (C.) serrata* Shelley (see Shelley 1984b, figs. 3-7, 19-22) in being expanded distally into a marginally serrated hood, partly shielding the structure carrying the prostatic groove, the solenomerite in the species of *Sigmoria.* This is a remarkable example of convergence, and as in *S. (C.) serrata* the eurymerodesmid hood is actually quite jagged. The margin is thickened, particularly on the lateral side, and in places there are up to three rows or layers of sharp, tiny teeth that line the inner margin overhanging the cavity as well as the outer border. Seen in profile from the proper perspective, the apex of the telopodite of *serratus* closely resembles a mitten, with the acropodite being the thumb and the hood representing the other fingers combined, which was the basis for Loomis' name, *planca.* The jagged nature of the distal margin is by far the dominant feature, and except for the inner prefemoral margin of *crassatus,* no other eurymerodesmid is even slightly irregular. Smooth gonopodal margins are the rule in this family.

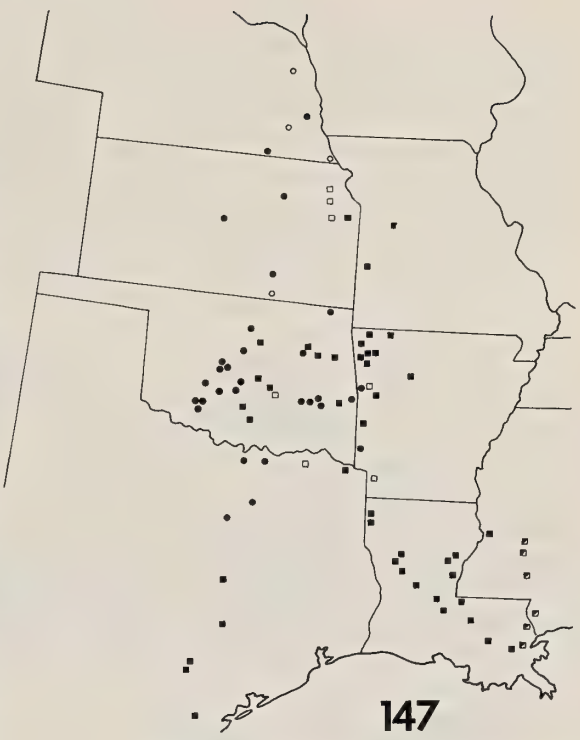


Fig. 147. Distribution of the *birdi* lineage. Squares, *birdi birdi;* half-shaded squares, *birdi planus;* dots, *mundus.* Open symbols denote literature records considered reliable.

The **Birdi** Lineage

The *birdi* lineage is characterized by continuous, broadly terminal, and poorly demarcated acropodites; sides of apertures undivided, without caudolateral pouches; and caudal margins either with densely hirsute lobes or comparatively dense hair patches in this location. Females cannot be reliably distinguished from those in other groups. In lobed forms the densest marginal hairs are on the projections, so when the latter are absent, the densest patches are usually at this general location, suggesting that pilosity is the sole remaining remnant. Forms with lobes also display variably elevated lateral margins, which tend to be lower in ones lacking projections; the lobes arise from the elevations, and in general as one becomes smaller so does the other. In populations of *birdi planus* in southeastern Louisiana, there is only a low, continuous marginal elevation extending around the caudolateral corner without a trace of lobes, and in the northernmost population, the aperture is strikingly unadorned with only modest hair patches at the caudolateral corners. The sides and caudal margin of this form are either flush with the metazonum or so slightly elevated as to appear flat in ventral view.

The *birdi* lineage contains two forms with strong lobes, *mundus* and the western populations of *b. birdi.* The lobes are rigid, inflexible structures, and

here they are very large, extending ventrad well below the levels of the adjacent coxae, suggesting impairment of motility and promotion of ecological and/or behavioral adaptations. I have not encountered either species, but for clearance, it seems that the lobes must alter the animal's posture. If they do not carry themselves high off the substrate, the lobes would seemingly become embedded or broken. I saw no individuals with broken lobes nor any in which the apical hairs had been scraped off, indicating that the structures are unaffected by motion. Meaningful observations and ecological studies on these eurymerodesmids are desirable because of these prominent structural features.

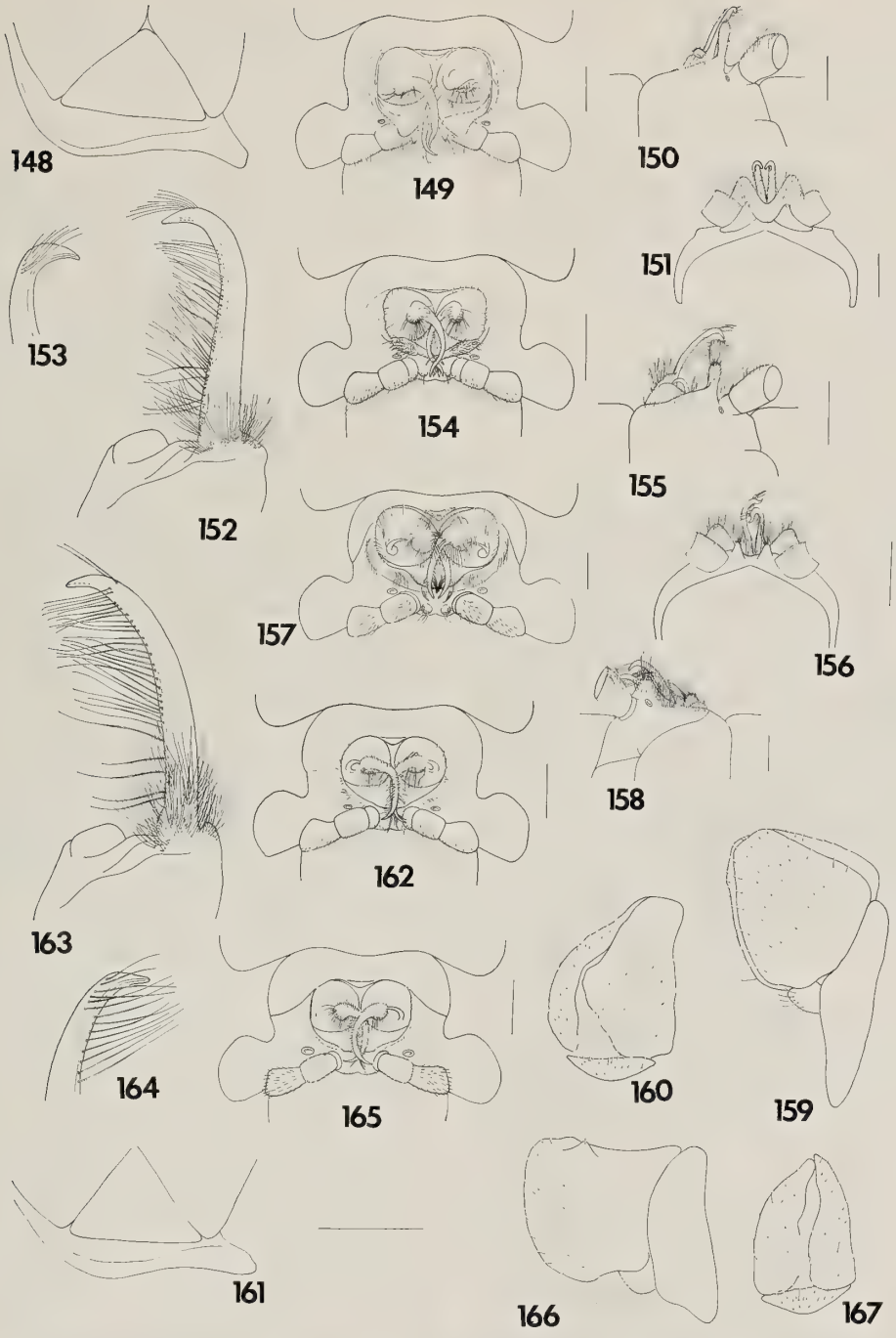
The *birdi* lineage, comprised of a single species group, the *birdi* group, is the northernmost in the family, extending from northeastern Nebraska and central Mississippi to the Gulf Coast of Louisiana and south-central Texas (Figs. 147, 213-214). Its area ranks second in size to that of the *varius* group, *Kewanius* lineage, but it contains only two species instead of five.

Components. — *birdi* Chamberlin [*b. birdi, birdi planus* Causey], *mundus* Chamberlin.

Eurymerodesmus birdi Chamberlin

Diagnosis. — A moderate-size species; males characterized by moderate to long mandibular projection; sides of aperture not divided, without caudolateral pouches, configuration variable, either flush with metazonal surface throughout, or elevating slightly, continuing around caudolateral corners, and descending a short distance along caudal margin, or elevating more strongly and continuing into variably long, broadly rounded, subtriangular lobes at caudolateral corners or on caudal margin; telopodite long; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners varying from slightly produced to elevated into short rim; receptacle large, sides not curved around operculum.

Remarks. — As represented by the types, the westernmost population of *birdi* possesses long aperture lobes that extend below the levels of the adjacent coxae. The projections are distinctive, easily recognized, and were adequately illustrated by Chamberlin (1931, fig. 8). This population occurs in Murray, Garvin, Seminole, and Pottawatomie counties, Oklahoma, and ones with equally long lobes occur sporadically to the east, for example in Vicksburg, Warren County, Mississippi. However, most forms outside these counties display variably shorter lobes, and there is a general trend toward smaller projections and lower marginal elevations as one proceeds southeastward in Louisiana. The lobes are also short north and south of these counties, but show no geographical trends. The projections disappear at New Orleans, leaving a low, uniform marginal elevation extending from the anterior halves of the sides around the caudolateral corners. In central Mississippi, the form named *planus* by Causey (1950b) exhibits an unadorned aperture without elevations but with modest hair patches at the caudolateral corners. The opening is flush with the metazonum, and the hair patches occur at the approximate position of the lobes. Southward towards New Orleans the sides and caudal margin begin to elevate, but always uniformly, without a trace of lobes. The evidence is not as convincing as in *varius,* where there is clear intergradation between *v. varius* and *v. christianus,* but I think that these forms with and without subtriangular lobes blend smoothly together, since forms in East Baton Rouge and West Feliciana parishes have very short lobes, barely detectable above the marginal elevations. Thus, *planus* is a form of *birdi,* the oldest name for this ensemble, and as first reviser, I assign *planus* to the populations lacking lobes, ranging essentially from New Orleans to near Jackson, Mississippi. The only other population showing reasonable anatomical stability is the one in central Oklahoma with large lobes represented by the types of *birdi.* However, if it is designated the nominate subspecies, the intergrade area will be vastly larger than that of either race, since the other three available names — *creolus, schmidti,* and *plishneri* — apply to forms in areas of high instability. This solution is impractical, and I therefore combine all forms with detectable lobes under the nominate subspecies, essentially everything north and west of New Orleans, including a few localities east of the Mississippi River. In contrast to *varius,* I do not recognize an intergrade region *per se* in *birdi* because this is virtually the entire range between New Orleans and central Oklahoma. Consequently, *birdi* is the most intricate eurymerodesmid next to *amplus,* since it encompasses the second greatest array of variants. Causey (1950b) was amply justified in considering *planus* a valid species, for it could hardly be more distinct from the types of *birdi.* However, these forms are merely opposite ends of a complex spectrum of lobed eurymerodesmids that Chamberlin (1931) was the first to name.



Figs. 148-167. *Eurymerodesmus birdi*. 148, projections of right mandible of holotype, lateral view. 149, aperture and gonopods *in situ* of holotype, ventral view. 150, the same, lateral view. 151, the same, caudal view. 152, left gonopod of the same, lateral view. 153, telopodite of the same, medial view. 154, aperture and gonopods *in situ* of male from Caddo Par., LA, ventral view. 155, the same, lateral view. 156, the same, caudal view. 157, aperture and gonopods *in situ* of male from Polk Co., AR, ventral view. 158, the same, lateral view. 159, left cyphopod of allotype, caudal view. 160, the same, lateral view. 161-167, *birdi planus*. 161, projection of right mandible of holotype, lateral view. 162, aperture and gonopods *in situ* of holotype, ventral view. 163, left gonopods of the same, lateral view. 164, telopodite of the same, medial view. 165, aperture and gonopods *in situ* of male from Pearl River Co., MS, ventral view. 166, left cyphopod of female from Simpson Co., MS, caudal view. 167, the same, dorsal view. Scale lines for figs. 149-151, 154-158, 162, and 165 = 1.00 mm. Line for other figs. = 0.30 mm for 148 and 161; 0.40 mm for 152, 163, and 166-167; and 0.50 mm for 153, 159-160, and 164.

Eurymerodesmus birdi birdi Chamberlin, new status
Figs. 147-160, 211-232

Leptodesmus hispidipes: Gunthorp, 1913:162 (in part). Chamberlin, 1918:370 (in part).

Eurymerodesmus birdi Chamberlin, 1931:101-102, figs. 6-8. Attems, 1938:185-186, figs. 204-205. Causey, 1952b:1-2. Chamberlin and Hoffman, 1958:79. Stewart, 1969:384.

Eurymerodesmus creolus Chamberlin, 1942a:6, pl. 2, fig. 16. Chamberlin and Hoffman, 1958:79. **NEW SYNONYMY.**

Eurymerodesmus schmidti Chamberlin, 1943:38, fig. 7; 1952:573. Causey, 1952b:2. Chamberlin and Hoffman, 1958:81. **NEW SYNONYMY.**

Eurymerodesmus plishneri Causey, 1950a:271, fig. 8. **NEW SYNONYMY.**

Type specimens. — Male holotype, one male paratype, and female allotype (NMNH) collected by R. D. Bird, 17 October 1929, from an unknown site in Murray Co., OK.

Diagnosis. — Apertures with distinct subtriangular lobes of varying lengths at varying positions along caudal margin to caudolateral corners.

Color in Life. — Peritremata orange; metaterga gray-brown with orange stripes along caudal margins connecting paranotal markings; collum with stripes along both anterior and posterior margins (Causey 1950a). Causey further states that the metatergal stripes are usually wider mediad, rendering a trimaculate appearance resembling the syntopic platyrhacid *Auturus evides* (Bollman). Chamberlin (1931, 1942a, 1943) also recorded the striped pattern, but from faded preserved specimens.

Holotype. — Body highly fragmented, length unmeasurable, maximum width 4.2 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.7 mm, interantennal isthmus 0.7 mm. Antennae missing, length and relative lengths of antennomeres unknown, recorded from paratype. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, subantennal 1-1, frontal 1-1, clypeal about 8-8, labral about 13-13. Projection of mandibular stipes long, stout, bluntly rounded (Fig. 148).

Collum extending slightly below ends of following tergite. Paranota depressed, continuing slope of dorsum; posterior corners rounded through segment 8, blunt on 9-13, becoming progressively more acute posteriorly.

5th sternum with broad, flattened, paramedian processes between both leg pairs; 6th sternum with subconical processes between both coxae. Postgonopodal sterna with subconical projections between 9th legs; remaining sterna with shorter subconical lobes on segment 8, becoming progressively flatter posteriorly with variable bicruciform impressions and variable hair tufts subtending coxae, becoming sparser caudally. 2nd coxa with short, rounded anterior, and longer, subacuminate caudal lobes. Prefemoral lobes extending through segment 16.

Gonopodal aperture (Figs. 149-151) subrectangular, without caudolateral pouches, with moderate anterior indentation, 1.8 mm wide and 0.7 mm long at maxima; anterior indentation short, broad, rounded; sides entire, nearly linear, becoming progressively more elevated caudad, leaning slightly over opening, rims essentially smooth; caudolateral corner broad, rounded; caudal margin continuous laterally with sides, extending immediately into enormous, broadly subtriangular lobe, leaning caudad, narrowly segregated in midline from opposite lobe and thus occupying nearly half of breadth of aperture, lobe extending well below margins of adjacent coxae, apex broad, rounded, perhaps 1/3 as wide as base, dropping to metazonal surface just before midline; margins irregularly hirsute with long hairs arising from rim or short distances down outer surfaces and overhanging opening, with several hairs on anterior indentation, scattered hairs on sides and caudolateral corner, hairs shorter and very dense on all surfaces of lobes, becoming slightly denser distad. Gonopods *in situ* (Fig. 149) with telopodites overlapping opposite member in midline, extending caudad between aperture lobes and terminating between 9th legs below level of apices of lobes. Gonopod structure as follows (Figs. 152-153): Telopodite terminating before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, linear for most of length, curving distad, sides parallel for most of length, tapering smoothly and continuously distad with two rows of continuous, regularly spaced hairs along inner margin and distomedial tuft of about six hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, continuing curvature of latter, sides tapering rapidly to acuminate tip.

Male paratype. — Body fragmented, length unmeasurable. Antennae reaching back to anterior half of 3rd metatergite, relative lengths of antennomeres 2>4>3>5=6>1>7. Somatic and gonopodal features closely similar to those of holotype.

Female allotype. — Length 22.2 mm, maximum width 3.6 mm, W/L ratio 16.2%. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal and frontal setal series absent. Projection of mandibular stipes short, blunt. Sterna relatively flat and unmodified, without projections, with only a few randomly scattered setae, especially along caudal margins.

Cyphopodal aperture subrectangular, caudal margin distinctly elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely, edges of valves and corner of receptacle visible in aperture, open side facing dorsad. Valves (Figs. 159-160) large, moderately hirsute, slightly unequal, anterior one larger, distal margins elevated into short rim. Receptacle large, glabrous, located laterad to valves, sides curving partly around operculum. Latter relatively large, located at bases of valves on dorsal side.

Variation. — Size varies markedly, with the smaller individuals occurring to the north in Missouri and Kansas and the largest specimens in Polk County, Arkansas. Elsewhere body proportions seem random and probably reflect habitat conditions. Piecing together males with no more than two fragments the following measurements were made:

Table 5. Size variation of *E. b. birdi* males.

State	County	Length (mm)	Width (mm)	W/L ratio (%)
Kansas	Douglas	22.0	3.4	15.5
Oklahoma	Payne	24.1	4.0	16.6
Oklahoma	Garvin	27.0	4.4	16.3
Arkansas	Washington	28.7	4.5	15.7
Arkansas	Polk	37.8	5.3	14.0
Louisiana	Natchitoches	33.9	5.0	14.7
Texas	Bowie	33.2	4.8	14.5

The gonopods are relatively constant throughout the range but the angle of projection from the aperture varies from nearly directly ventrad with the tips leaning slightly between the aperture lobes, to caudad, with the apices extending directly between and beyond the lobes, and overhanging the sternum between the 9th legs. On the apertures, considerable variation obtains in the configurations of the lateral margins, the size and degree of separation of the caudal lobes, and the hirsuteness of the lateral and caudal margins. Since the lobes are the most prominent feature, differences in their relative proportions are particularly noticeable, and I analyzed this geographically. The longest lobes occur primarily in forms along the western range periphery, around the type locality in central Oklahoma, where all males exhibit them. Elsewhere they are random. These lobes are moderately hirsute, much longer than the widths of the 9th coxae, usually extend ventrad below the telopodites, are relatively broad, and are narrowly segregated in the midline. Together they comprise most of the caudal margin of the aperture and are aligned with the sternal processes between the 9th legs (Fig. 151). Thus, a subspecies could be recognized from Seminole, Pottawatomie, Murray, and Garvin counties, Oklahoma, but elsewhere the lobes vary randomly and capriciously with too little stability, even within single populations as reflected by the larger samples, to justify taxonomic recognition. In the most common configuration (Figs. 154-156), the lobes are subequal to or only slightly longer than the 9th coxae, do not extend ventrad below the telopodites, and are more widely segregated thus being situated more laterad, at or partly on the caudolateral corners, and "outside" the succeeding sternal processes as seen in caudal profile (Fig. 156). However, this form intermingles sporadically with ones with shorter lobes located either more laterad or mediad (Figs. 157-158), and the male from Mississippi has long lobes like the form in central Oklahoma. In the male from East Baton Rouge Parish, Louisiana, the lobes are situated at the caudolateral corners and are so widely segregated that the caudal margin seems to lack them. A specimen from Grand Ecore, Natchitoches Parish, exhibits a uniformly elevated caudal margin without a trace of lobes, as in *b. planus,* but the other male in this sample has prominent lobes. Males from West Feliciana and Jefferson parishes show very small lobes, only slightly higher than the marginal elevations, and those in south Texas are small to moderate-size, with extremely long hairs in some individuals. Finally, the lobes are not always equal in a single individual; in a few males, one is clearly longer than the other. Thus, aside from central Oklahoma, *b. birdi* does not exhibit a consistent set of features, thus obviating additional races. If future studies indicate otherwise, *creolus* has priority over both *schmidti* and *plishneri.*

Aside from the length and position of the lobes, they can also extend either directly ventrad or lean anteriad or caudad, accordingly creating narrower or broader openings. Where they lean anteriad, the aperture appears wider along the anterior margin. The degree of hirsuteness of the lobes and the lateral margins vary, and some males are exceptionally hairy with long, matted hairs, nearly as long as the lobes themselves, extending from their tips and anterior and caudal margins (Fig. 155). On the sides of the apertures, hairs arise mostly from the rim, but on sporadic individuals they also extend varying distances down the outer surface (Figs. 157-158). These lateral marginal hairs can also be very long, overhanging up to perhaps 1/4 of the width of the aperture.

The lateral elevations also vary, in many individuals arising smoothly and continuously beginning at the anterolateral corners and curving around the caudolateral corners into the lobes. In other males the elevations begin a short distance back of the anterolateral corners, producing a "stepped" effect in conjunction with the lobes. in some such individuals, the elevated parts of the lateral margins lean inward over the opening, causing it to appear wider along the anterior border.

Ecology. — The specimen reported by Chamberlin (1942a) was collected under a log in Caddo Parish, Louisiana; Causey (1950a) mentioned that oaks were dominant at the six recorded localities of *plishneri* in Washington and Carroll counties, Arkansas. The following habitat data was indicated on vial labels: on a driveway (Payne Co., OK); on a patio (Garvin Co., OK); under rocks in woods (Wagoner Co., OK); in an old stump, in rocks, and in water wells (Natchitoches Par., LA); under logs (Caddo Par., LA); in hardwoods at a lumber yard (West Feliciana Par., LA); and in sandy post oak soil (Wilson Co., TX). The milliped was collected in caves in Seminole, Cherokee, and LeFlore counties, Oklahoma, one of three eurymerodesmids known from subterranean habitats along with *oliphantus* and *melacis.* These areas are either on the western periphery of the Ozark and Ouachita Provinces or the eastern fringe of the Central Plains and may or may not represent accidental records.

Distribution. — From the southern Central Lowland Physiographic Province south of the Missouri River in northeastern Kansas and central Missouri, through the western Ozark Plateau and Ouachita Provinces to northeast Texas and the southern Mississippi Valley, with additional, possibly allopatric, populations in south-central Texas on the western fringe of the Coastal Plain (Figs. 147, 211-212). Specimens were examined as follows:

KANSAS: *Douglas Co.,* Lawrence, 3M, September 1977, R. Graham (RLH); and Univ. of Kansas Nat. Hist. Res., M, 2F, 29 September 1961, R. C. Funk (EIU) and 3M, 4 October 1966, D. Clark (FSCA). *Johnson Co.,* 3 mi. E. Eudora, M, 4 October 1966, D. Clark (FSCA).

MISSOURI: *Johnson Co.,* Knob Noster, 2M, 7F, 29 September 1962, and 11M, 25 F, November 1962, E. Peterman (FSCA). *Vernon Co.,* Nevada, M, 1 October 1961, D. J. McReynolds (MCZ).

OKLAHOMA: *Cherokee Co.,* 3 mi. SE Ft. Gibson Dam, Dressler Cave, 5M, F, 21 March 1971, J. H. Black (FSCA). *Wagoner Co.,* Lake Bixhoma, M, 1 March 1975, J. M. Nelson (NCSM). *Payne Co.,* Stillwater, M, 15 March 1984, R. M. Edwards (OKSU). *Pottawatomie Co.,* Dale, M, 3F, September 1954, Brown (FSCA). *Seminole Co.,* locality unknown, M, May 1931, P. Newport (SMUO); and Whiskey Cave, M, 6 January 1974, J. H. Black (FSCA). *Garvin Co.,* locality unknown, 4M, F, 2 November 1984, B. Lucas (OKSU). *Murray Co.,* locality unknown, 2M, F, 17 October 1929, R. D. Bird (NMNH) TYPE SPECIMENS, and 2M, F, 3 juvs., 17-26 October 1928, R. D. Bird (SMUO); Sulphur, M, 18 April 1976, W. Magdych (SMUO); and near Turner Falls, Arbuckle Mts., M, 23 April 1936, L. Hubricht (NMNH). *LeFlore Co.,* 10 mi. NE Talihina, Bear Den Cave, 4M, 17 November 1973, J. H. Black (FSCA).

ARKANSAS: *Benton Co.,* 5 mi. E Siloam, Chamber Spgs. Ranch, 3M, 2 September 1955, C. E. Hastings (FSCA); and Bella Vista, 2M, 13 April 1962, H. Hart (FSCA). *Carroll Co.,* Blue Springs, 3M, F, 29 October 1949, N. B. Causey (FSCA). *Washington Co.,* Springdale, Eden's Bluff, 3M, 8F, 2 juvs., 1 October 1949, N. B. Causey (FSCA); Fayetteville, M, 8 April 1959, N. B. Causey (FSCA), Mt. Kessler, M, F, 11 April 1949, N. B. Causey (ANSP) and 2M, F, 3 November 1949, collector unknown (FSCA), and Univ. of Arkansas campus, 2M, 10 February 1953, L. Jackson (FSCA); nr. Prairie Grove, Cove Cr. Valley, 18M, 23F, 4 juvs., 1 November 1955-25 March 1960, M. Hite (FSCA); and Devil's Den St. Pk., M, 3F, 2 juvs., 29 September 1948, N. B. Causey (FSCA) and M, December 1963, N. B. Causey (MCZ). *Pope Co.,* locality unknown, M, 6 February 1955, B. Bowie (FSCA). *Logan Co.,* along AR hwy. 23 nr. Booneville, M, 19 November 1966, M. Hite (FSCA). *Polk Co.,* Rich Mtn., Mena, 11M, 2F, 21-22 March 1938, K. P. Schmidt (FMNH, NMNH), and 5M, 7F, 1950-May 1956, A. McWilliams and N. B. Causey (FSCA).

MISSISSIPPI; *Warren Co.,* Vicksburg, M, 7 February 1933, O. F. Cook (NMNH).

LOUISIANA; *Caddo Par.,* 5 mi. NW Shreveport, M, 13 April 1936, L. Hubricht (NMNH); and Shreveport, 3M, 9F, 3 juvs., 24 March 1962, N. B. Causey (FSCA). *Natchitoches Par.,* locality unknown, 25M, 13F, October 1954-February 1956, various collectors (FSCA); Natchitoches, Northwestern State Univ. campus, 7M, 12F, 3 juvs., February 1954-March 1956, J. E. Sublette and C. Morehead (FSCA); and 16 mi. SSE Natchitoches, 2M, 3F, 16 October 1965, D. E. Hahn (FSCA). *Rapides Par.,* along LA hwy. 28, 8.8 mi. E Gardner, 8M, 7F, 7 November 1965, R. E. Tandy and L. D. Wilson (FSCA). *Concordia par.,* Tensas R., 2M, 1954, B. Stanberry (FSCA). *Avoyelles Par.,* Evergreen, 2M, 4F, 28 October 1965, M. Kordisch (FSCA). *Evangeline Par.,* 2.5 mi. S Chicot St. Pk., M, 2F, juv., 30 January 1968, E. D. Kaiser (FSCA). *St. Landry Par.,* along LA hwy. 10, 2 mi. W Mellville, M, 3F, 24 March 1965, R. Tandy (FSCA). *East Baton Rouge Par.,* Louisiana St. Univ. Campus, M, November 1971, collector unknown (FSCA). *West Feliciana Par.,* locality unknown, M, F, 18 March 1962, L. Hubricht (RLH). *Jefferson Par.,* Narahan Jct., Elmwood Plantation along River Rd. at Research Dr., 0.3 mi W jct. US90, 2M, 2F, juv., 17 February 1986, R. M. Shelley (NCSM).

TEXAS: *Bowie Co.,* along US hwy. 259, 5 mi. S Red River, M, 9 December 1967, T. C. Stewart (SFAU). *Bell Co.,* Belton, M, January 1931, collector unknown (NMNH). *Bastrop Co.,* Bastrop St. Pk., 2M, 2 April 1960, J.C. Loomis (RLH). *Wilson Co.,* 8 mi. N Floresville, 2M, 29 April 1961, collector unknown (FSCA); and 8 mi. N Stockdale, M, 6 April 1961, J. F. Quinlan (FSCA). *San Patricio Co.,* Lake Corpus Christie St. Pk., M, 2 July 1969, J. R. Heitzman (FSCA).

The following literature records of additional localities are believed to refer to *b. birdi* and are so indicated in figures 147 and 211-212.

KANSAS (Gunthorp, 1913, cited as *Leptodesmus hispidipes): Jefferson Co.,* no further data.

OKLAHOMA (Causey 1952b); *Hughes Co.,* no further data.

ARKANSAS (Causey 1952b): *Sebastian Co.,* no further data. *Miller Co.,* no further data.

LOUISIANA (Chamberlin 1918, cited as *Leptodesmus hispidipes): Natchitoches Par.,* Creston.

TEXAS (Stewart 1969): *Lamar Co.,* 8 mi. SE Paris.

Additional samples with a male from White Rock, Arkansas (FSCA), and a male and several females from Pacheco, Texas (FSCA), cannot be located in maps or gazetters of these states.

Remarks. — The males from Norman, Cleveland County, Oklahoma (SMUO), which Chamberlin designated paratypes of *birdi* are actually specimens of *mundus.*

The label with the sample from 8 mi. N Floresville, Wilson Co., TX, states that the milliped was "very common, usually paired and grouped," but does not indicate whether the pairing was between opposite sexes.

The male from Payne County, Oklahoma (OKSU), has an accessory gonopod at the right anterior position of segment 8, the first example of heteromorphosis in the Eurymerodesmidae. The structure is shorter than normal and enclosed within a small circular aperture that does not extend across the midline. The lateral margin is normally elevated and extends into a typical caudal lobe, subequal in length to those on segment 7. A normal leg occurs opposite the accessory gonopod at the left anterior position of segment 8.

Eurymerodesmus birdi planus Causey, new status
Figs. 147, 161-167, 211

Eurymerodesmus planus Causey, 1950b:196-197, fig. 5. Chamberlin and Hoffman, 1958:80.

Type specimen. — Male holotype (ANSP) collected by S. Bender, 13 April 1950, from Piney Woods, Rankin Co., MS. According to Causey (1950b) the type series also contained three females, now lost.

Diagnosis. — Apertures without lobes at any position, usually with denser hair patches at caudolateral corners, with or without uniform marginal elevations, arising on anterior halves of sides, curving around caudolateral corners, terminating before midline on caudal margin (Figs. 162, 165).

Color in life. — Paranota orange; metaterga dark with orange stripes along caudal margins connecting paranotal markings; collum with orange stripes along both anterior and posterior margins (Causey 1950b). Causey also mentioned the presence of a roughly triangular median orange spot on some metatergites, perhaps reflecting expansion of the stripe in the midline, and several small, confluent orange dots on others. A paratype female had "two to six" orange dots on the metatergites.

Variation. — All specimens were tightly coiled and would not unroll without fragmenting into two or more pieces. A male from Pearl River County, Mississippi, which only broke into two pieces, measured approximately 24.0 mm long, 3.4 mm wide, W/L ratio 14.2%.

As stated, the holotype exhibits an unadorned aperture, margins being flush with the metazonum. Its only attributes are modest hair patches at the caudolateral corners, which really are nonexistant since the sides curve strongly mediad. Consequently, the aperture is proportionately the smallest in the genus and is heart-shaped in overall appearance (Fig. 162). The gonopods are a little more curved than the linear ones of the nominate subspecies (Figs. 163-164).

The Simpson County males from Braxton are near topotypes, occurring just across the county line from the type locality. Here the sides of the aperture are slightly but distinctly elevated beginning at the anterolateral corners. In the males from Jefferson Davis County, the caudolateral corner is angled and slightly more elevated; thus the caudal margin slopes downward from the corner, meeting the metazonal surface in the midline. Essentially the same condition obtains in the Pearl River County males (Fig. 165), except the caudolateral corner is rounded and leans over the aperture in one male. All Mississippi males exhibit hairs at the caudolateral corners, their densities and lengths varying, being longest in the last sample.

The Louisiana males display essentially the same conditions as those from southern Mississippi. In the St. Tammany Parish specimens, the moderately elevated sides continue around a squared caudolateral corner, then slope to the metazonal surface near the midline. In that from New Orleans, the sides are essentially flush with the metazonal surface, with the caudolateral corner being slightly elevated and rounded. The caudal margin extends slightly in the midline in all Louisiana males, and the hairs continue a short distance beyond the caudolateral corner in the New Orleans male.

The mandibular projection of the holotype is shorter and broader than in the nominate race (Fig.

161). The female genitalia are closely similar to those of *b. birdi* (Figs. 166-167).

Ecology. — The samples from Pearl River County Mississippi, were collected in "flood plain, water oaks." Those from 2.5 miles south of Prentiss, Jefferson Davis County, were retrieved from a pitfall trap on a hillside in pine woods.

Distribution. — The southern Gulf Coastal Plain of Mississippi and southeastern Louisiana, ranging from Jackson to New Orleans (Figs. 147, 211). Specimens were examined as follows:

MISSISSIPPI: *Rankin Co.,* Piney Woods, M, 13 April 1950, S. Bender (ANSP) TYPE LOCALITY. *Simpson Co.,* near Braxton, 2M, 5F, 4 juvs., 1 April 1958, S. Lazell (FSCA); and Mendenhall, M, 2 January 1960, L. Hubricht (RLH). *Jefferson Davis Co.,* 3 mi. SSW Prentiss, along White Sand Cr., 2M, 25 December 1959, L. Hubricht (RLH); and 2.5 mi. SW Prentiss, 4M, 27 February 1987, P. K. Lago (RLH). *Pearl River Co.,* 11 mi. E Bogalousa, LA, 6M, 4F, 21 January 1965, N. B. Causey (FSCA).

LOUISIANA: *St. Tammany Par.,* Talisheek, along Talisheek Cr., 2M, 12 December 1965, L. D. Wilson (FSCA); and 1 mi. W Talisheek, 2M, 9 February 1939, collector unknown (NMNH). *Orleans Par.,* New Orleans, city park, M, 20 February 1950, collector unknown (FSCA).

Eurymerodesmus mundus Chamberlin
Figs. 147, 168-175, 211-212

Leptodesmus floridus: Kenyon, 1893:16.
Leptodesmus hispidipes: Gunthorp, 1913:162 (in part).
Eurymerodesmus mundus Chamberlin, 1931:102-103, figs. 3-5. Attems, 1938:186-187, fig. 206. Causey, 1952b;2. Chamberlin and Hoffman, 1958:80.

Type specimens. — Male holotype and male paratype (NMNH) collected by D. Zeigler, 26 February 1930, at University (Norman), Cleveland Co., OK. One male paratype (NMNH) collected by R. D. Bird, 5 April 1929, at an unknown site in Cleveland County.

Diagnosis. — A moderate-size species; males characterized by long mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating slowly around caudolateral corners onto caudal margin, extending into very large clavate lobes; telopodite long; acropodite short, about 1/8 of acropodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner surface; cyphopod valves of females with distal corners slightly produced; receptacle moderate size, sides curving around operculum.

Color in Life. — Paranota red; metaterga brown with concolorous stripes along posterior margins connecting paranotal markings; collum with brick red stripes along both anterior and posterior margins (Chamberlin 1931). All specimens available to me were preserved with faded colors, but many still showed clear evidence of this striped pattern.

Holotype. — Body fragmented, length unmeasurable, maximum width 4.1 mm.

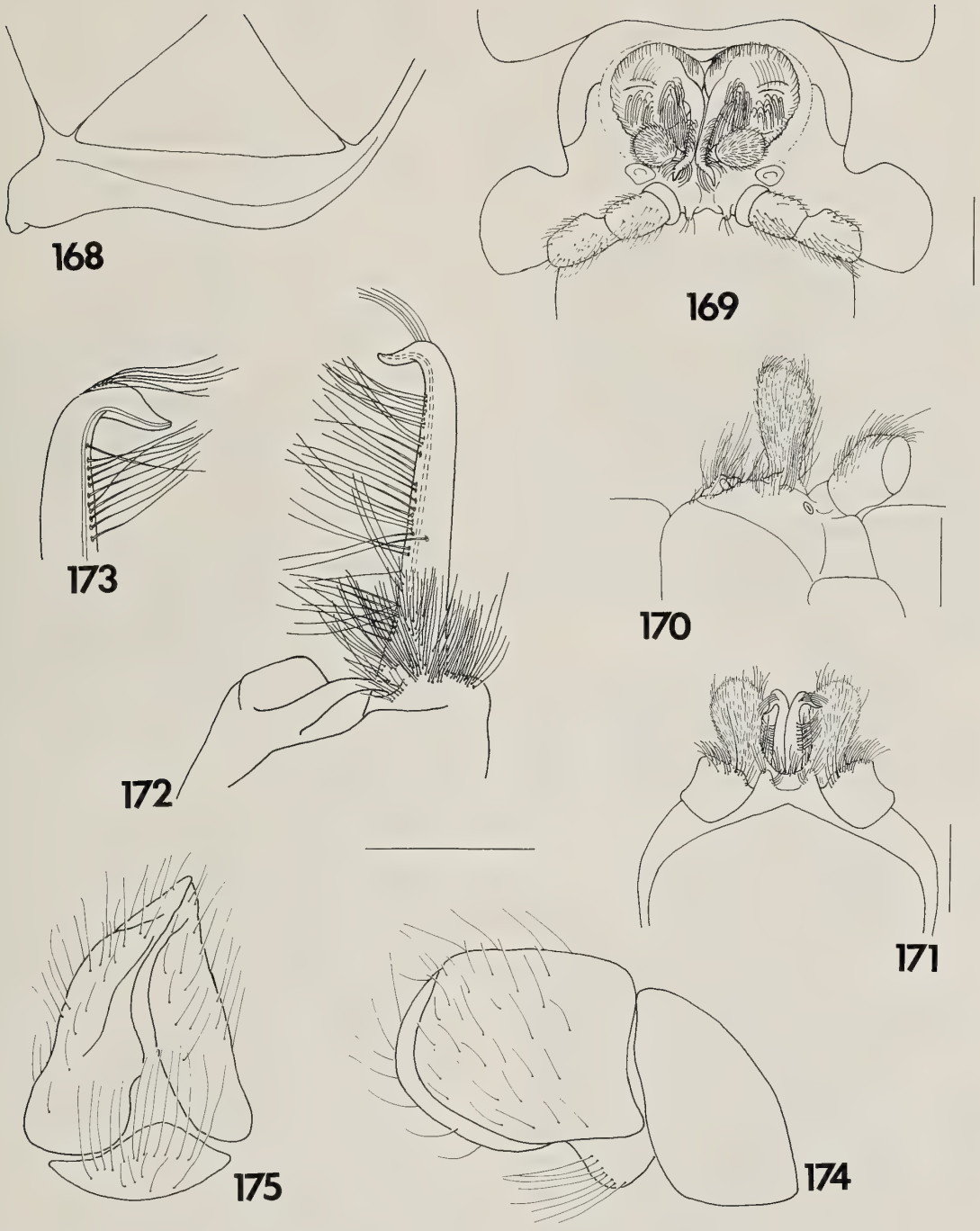
Somatic features similar to those of *E. hispidipes,* with following exceptions:

Width across genal apices 3.2 mm, interantennal isthmus 0.8 mm. Relative lengths of antennomeres 2>3>5>4>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent; clypeal about 11-11, labral about 14-14. Projection of mandibular stripes long and broad, ventral margin indented, tip smoothly irregular (Fig. 168).

Collum extending slightly below ends of following tergite. paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 8, blunt on 9-14, becoming progressively more acute posteriorly.

5th sternum with short, widely separated knob-like processes adjacent to leg coxae; 6th sternum with broader, shorter, paramedial projections, caudal ones longer. Postgonopodal sterna with narrow, rounded, widely segregated lobes between 9th legs; remaining sterna with widely separated subconical lobes on segment 8 and flattened, elevated areas on 9, becoming progressively flatter posteriorly with variable transverse impressions between leg coxae, and shallow, faint to moderate central impressions rendering somewhat bicruciform appearance, all except 18th sterna with tufts of setae on ventral surfaces adjacent to leg coxae. 2nd coxa with large, rounded anterior, and narrower subconical posterior lobes. Prefemoral lobes extending through segment 16.

Gonopodal aperture (Figs. 169-171, not this specimen) ovoid, widest along anterior margin, without caudolateral pouches, with slight anterior indentation, 1.9 mm long and 0.8 mm wide at maxima; anterior indentation short, broadly rounded; sides curving mediad, not divided, rising slowly and progressively to caudolateral corner, rims slightly irregular; caudolateral corner indistinct, continuing curvature and rise of sides; caudal margin continuous through caudolateral corner with sides, lowly elevated for short distance then extending greatly ventrad into an enormous, clavate, lobe extending ventrad well beyond level of coxae, dropping to level of marginal elevation and curving across midline, lobes paramedian and narrowly segregated in midline, aligned just outside sternal processes between 9th legs; margins heavily hirsute with hairs arising regularly from rim and overhanging opening, thicker along anterior indentation, also arising from outer surfaces laterally and caudally, caudal lobes densely pilose, hairs beginning basally and becoming denser apically, hairs on lobes much shorter and denser than those from aperture rim. Gonopods *in situ* (Fig. 169, not this specimen) with telopodites touching or nearly so in midline, extending between, and terminating just beyond aperture lobes, apices directed sublaterad. Gonopod structure as follows (Figs. 172-173): Telopodite terminating well before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, configuration linear, curving abruptly distad, sides parallel for most of length, tapering distad near level of curve, with two rows of continuous, regularly spaced hairs along inner margin culminating in slightly thicker tuft of six hairs, and distomedial tuft



Figs. 168-175. *Eurymerodesmus mundus*. 168, projection of left mandible of holotype, lateral view. 169, aperture and gonopods *in situ* of male from Comanche Co., OK, ventral view. 170, the same, lateral view. 171, the same, caudal view. 172, left gonopod of holotype, lateral view. 173, telopodite of the same, medial view. 174, left cyphopod of female from Canadian Co., OK, caudal view. 175, the same, dorsal view. Scale line for figs. 169-171 = 1.00 mm. Line for other figs. = 0.30 mm for 168, 0.40 mm for 172, and 0.50 mm for 173-175.

of about 6 hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, smoothly continuous with, and poorly demarcated from latter, bending sharply sublaterad, slightly bisinuate, sides tapering rapidly to acuminate tip.

Male paratype. — Agreeing closely with holotype in all particulars.

Female from Canadian Co., OK. — Length about 19.6 mm, maximum width 3.3 mm, W/L ratio 16.8%. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal setae 1-1, frontal setae 1-1. Mandibular stipes with minute rounded process. 3rd and 4th segments with moderate flanges lateral to legs. Sterna relatively flat and unmodified, without projections or tufts of setae.

Cyphopodal aperture subrectangular, caudal margin slightly elevated above metazonal surface. Cyphopods *in situ* with valves directed mediad, edges and side of receptacle visible in aperture, open side facing dorsad. Valves (Figs. 174-175) moderate-size, slightly unequal, anterior one larger and rounded, distal corners slightly produced. Receptacle moderately large, glabrous, located laterad to valves, sides curving partly around operculum. Latter relatively large, located at bases of valves on dorsal side.

Variation. — Size varies markedly, with larger specimens occurring in the center of the range from Oklahoma to Arkansas, and smaller ones occurring peripherally. Piecing together a few of the less fragmented males, with no more than two pieces, the following measurements were made. For most specimens merely straightening for measurement resulted in breakage.

Table 6. Size Variation of *E. mundus* Males.

State	County	Length (mm)	Width (mm)	W/L (%)
NE	Jefferson	21.9	3.2	14.6%
KS	Riley	22.4	2.9	12.9%
OK	Cleveland	31.1	5.0	16.1%
OK	Comanche	32.4	4.6	14.2%
AR	Sevier	33.9	5.6	16.5%
TX	Johnson	21.4	2.6	12.1%

The pregonopodal legs are more densely hirsute than those in the midbody region on some males, and in these individuals the legs become progressively less hirsute caudad. In some males the lateral margins of the gonopodal aperture are slightly excavated on the anterolateral corners. The distance between the caudal lobes varies, some being more widely segregated than others. In most individuals, the projections extend essentially directly ventrad, but in a few they diverge slightly laterad. These features occur randomly throughout the range. The lobes are virtually identical in length and configuration on all males except for the southernmost from Johnson County, Texas, where they are noticeably shorter and less clavate.

Ecology. — The holotype was collected in a "black jack forest" (Chamberlin 1931), presumably blackjack oak litter, on or very near the University of Oklahoma campus. Vial labels with habitat notations are as follows: under a litter and under rocks in the Wichita Mountains (Comanche Co., OK), on the floor of a house (Tulsa Co., OK), under a log (Noble Co., OK), in a storm cellar (Grayson Co., TX), and under a rock in a pasture (Ellsworth Co., KS).

Distribution. — *Eurymerodesmus mundus* is the northernmost species with presumably reliable literature records from northeastern Nebraska and one with a voucher specimen from near Omaha. The known distribution covers the Central Lowland Physiographic Province from northeastern Nebraska to the Brazos River in northern Texas, extending eastward into the Ouachita and Coastal Plain Provinces in eastern Oklahoma and southwestern Arkansas (Figs. 147, 211-212). Neither *mundus* nor the family is known from north of the Missouri River. Discovery in western Missouri south of this watercourse is anticipated. Specimens were examined as follows:

NEBRASKA: *Cass Co.,* South Bend, 2M, date unknown, F. C. Kenyon (NMNH). *Jefferson Co.,* Reynolds, M, 7 October 1981, W. F. Rapp (MCZ) and M, 9 September 1987, W. F. Rapp (RLH).

KANSAS: *Riley Co.,* locality unknown, 2M, 2 April 1952, L. Warren (FSCA) and Manhatten, M, 2 May 1940, H. H. Walker (RLH). *Ellsworth Co.,* 6 mi. SW Ellsworth, M, 2 May 1976, C. L. Starr (UGA). *Butler Co.,* 8 mi. SE Augusta, M, 14 October 1935, Burt (NMNH).

OKLAHOMA: *Craig Co.,* 1 mi. S Kansas state line, F, 7 April 1973, J. H. Black (FSCA). *Tulsa Co.,* Bixby, M, 1 December 1980, J. M. Nelson (NCSM). *Noble Co.,* Perry, M, 11 May 1967, D. C. Arnold (WAS). *Logan Co.,* 5 mi. NE Guthrie, M, 28 October 1959, R. C. Harrel (FSCA). *Canadian Co.,* locality unknown, 5M, F, 1930, N. M. Newport (SMUO) and Yukon, M, 1930, N. M. Newport (SMUO). *Caddo Co.,* locality unknown, 3M, F, February 1934, Carpenter (SMUO). *Grady Co.,* Chickasha, F, 4 June 1944, L. Hook (FSCA). *Comanche CO.,* Wichita Mts., locality unknown, 2M, 16 October 1971, collector unknown (MSU), Mt. Scott, MM, FF, 25 October 1974, G. Beck (MSU); Sunset Rec. Area, 2M, 29 October 1977, J. C. Cokendolpher and D. Parmley (MSU); Camp Boulder, F, 2 juvs., 8 June 1928, collector unknown (NMNH); and Panther Cr. Rec. Area, M, 6 November 1977, D. Parmley and K. Brice (MSU). *Cleveland Co.,* locality unknown, M, 5 April 1929, R. D. Bird (NMNH) and 2M, 20 February 1931, R. D. Bird (SMUO); and Norman, University, M, 10 March

1929, R. D. Bird (SMUO), M, 20 February 1937, D. Zeigler (NMNH) and M, March 1976, W. D. Butcher (SMUO) TYPE LOCALITY. *McClain Co.,* locality unknown, M, F, February 1933, Rosenmal (SMUO). *Pittsburg Co.,* McAlester, 2M, 2F, 10 February 1952, O. Murray (FSCA); and 3 mi. E Krebs, M, 2F, 22 October 1961, R. C. Harrel (FSCA). *Latimer Co.,* locality unknown, M, F, 25 April and 27 June 1931, R. D. Bird (SMUO) and 2M, F, 9 December 1933, Carpenter (SMUO); 5 mi. NW Wilburton, Robbers Cave St. Pk., M, F, 17 May 1960, R. C. Harrel (FSCA) and M, 25 October 1976, J. C. Cokendolpher (MSU); and Wilburton, M, 3F, 17 November 1934, Carpenter (ILNHS, SMUO). *LeFlore Co.,* 3.5 mi. N Howe, M, F, 26 May 1966, L. Hubricht (RLH).

ARKANSAS: *Polk Co.,* Rich Mt., Queen Wilhemina St. Pk., 2M, 8 November 1966, collector unknown (FSCA). *Sevier Co.,* Horatio, 4M, 8F, 11-15 April 1955 and 5 April 1956, C. N. Griffith (FSCA).

TEXAS: *Cooke Co.,* nr. old Townsite of Lea, M, 11F, 7 May 1968, collector unknown (FSCA). *Dallas Co.,* Dallas, 2M, 2F, June 1955, O. Sanders (FSCA); and between Duncanville and Cedar Hill, M, 3 November 1927, O. F. Cook (NMNH). *Johnson Co.,* Cleburne St. Pk., M, 26 December 1979, G. Spicer (NCSM).

The following additional literature records are believed to refer to *mundus* and are so indicated in figure 147.

NEBRASKA (Kenyon 1893, cited as *Leptodesmus floridus,* a synonym of *Semionellus placidus* (Wood) (Chamberlin and Hoffman 1958)): *Cuming Co.,* West Point. *Lancaster Co.,* Roca. *Richardson Co.,* Rulo. *Unknown county,* La Platte.

KANSAS (Gunthorp 1913, cited as *Leptodesmus hispidipes): Cowley Co.,* no further data.

Remarks. — Labels in the holotype and paratype vials read *"Erymnogon" mundus* rather than *Eurymerodesmus,* indicating that Chamberlin originally thought this species required a new genus. The lobes probably created this impression, but he must have changed his mind, and fortunately *"Erymnogon"* was never validated, although it would have been available as a subgeneric designation for the *birdi* lineage. However, Chamberlin did incorrectly designate a male topotype in the SMUO as a paratype of *birdi.*

The sample from South Bend, Nebraska, collected by F. C. Kenyon, the northernmost known for the family, is identified as *"Leptodesmus floridus."* This was not among the Nebraska localities Kenyon (1893) reported, but those he did — West Point, Rulo, Roca, and La Platte — probably also refer to *mundus.* Thus, I include his usage of *L. floridus* in the synonymy. The first three sites are indicated by open symbols in figure 147; the last is not on the official Nebraska map. Hence, the range for *mundus* probably extends north of the Platte River. I also include under *mundus* the Kansas records of *Leptodesmus hispidipes* by Gunthorp (1913), since they are either in or near the known range and likely refer to this species.

Chamberlin (1931) characterizes the lobes as arising from the sternum behind the gonopods, but his description of laminas extending ectad and cephalad from the structures implies that they are part of the aperture margin.

In addition to being the northernmost congener, *mundus* also forms the western boundary of the family in the northern part of the range (Fig. 147). The Missouri River seems to be a boundary, not only for *mundus* but also for the family. No eurymerodesmids have been taken to the north of this river in Iowa and northern Missouri. Consequently, I doubt if *mundus* occurs in the southeastern corner of South Dakota.

The **Melacis** Lineage

Located primarily in south and central Texas, on the known southern and western peripheries of the generic and family range, the *melacis* lineage is a nondescript assemblage with few distinguishing features. It is best characterized negatively, as the assemblage in Texas with short acropodites that lacks aperture lobes and pouches, and whose lateral margins are undivided. Common traits are small body size and short telopodites, which are either wholly enclosed by the aperture or just overlap the caudal margin, unless the specimen is exceptionally compressed. The apertures are comparatively small in three species, but *dactylocyphus* has proportionally the largest openings in the family. *Eurymerodesmus digitatus,* with intermediate-size openings, bridges the anatomical gap. Aperture margins are the most unmodified in the family; the sides are entire, and there are no lobes, pouches, or flares. Again *dactylocyphus* is an exception, with cupped, flange-like elevations at the caudolateral corners and adjoining parts of the sides and caudal margin, and again, *digitatus* spans the anatomical gap, at least in some populations. Although the telopodites are short, barely extending beyond the caudal aperture margin, the relative proportions of the prefemur and acropodite are as in the *birdi*

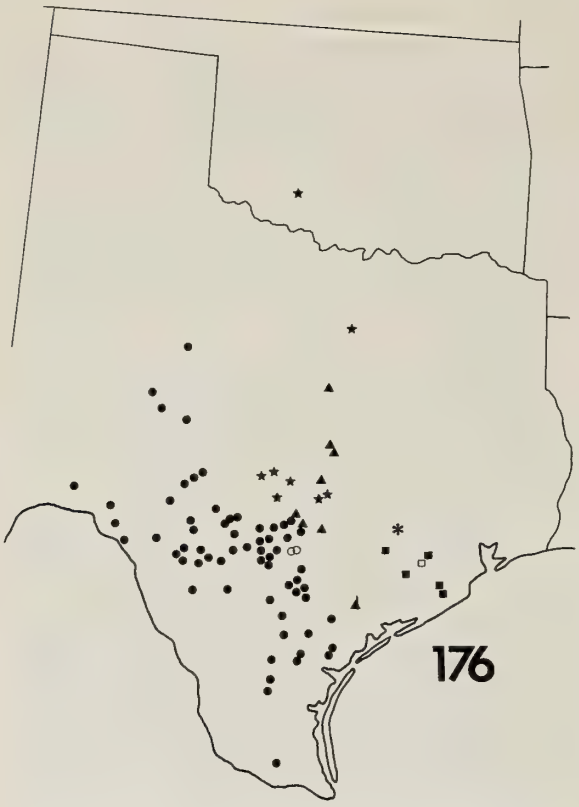


Fig. 176. Distribution of the *melacis* lineage. Dots, *melacis;* triangles, *dactylocyphus;* squares, *sanbernardiensis;* stars, *digitatus;* asterisk, *clavatus.* Open symbols denote literature records considered reliable.

lineage and *varius* group, with the prefemur constituting from 2/3 to 7/8 of the telopodite length. Acropodites are broadly terminal and continuous with the prefemur except for *clavatus,* where it is narrowly terminal, discontinuous, and sharply demarcated, arising from the outer prefemoral margin. This condition, accompanied by a clavate prefemur with a shoulder on the inner distal margin, is the obverse of that found in *simplex,* where the shoulder is on the outer surface, and the acropodite arises from the inner surface. Females do not display distinguishing features enabling them to be reliably identified, except again for *dactylocyphus* and to a lesser extent *digitatus.* The former possesses variable valvular projections ranging from small, nubbinlike papillae in eastern populations to long, flexible dactyliform structures in western forms that extend caudad and overhang two to three segments. This dactyliform condition is convergent with that in *compressus,* with the important distinction that the projections are flexible instead of being stiff and rigid. Thus the *melacis* group is characterized by small body size (all species); short telopodites (all species); terminal, continuous acropodites (excepting *clavatus*); small, unadorned apertures (excepting *dactylocyphus*); and rather nondescript, unadorned cyphopod valves (excepting *dactylocyphus*).

Located in south Texas, south of and parapatric to most of the *varius* group, with an extension into southwestern Oklahoma, the *melacis* lineage is the only eurymerodesmid component that may extend into Mexico. Since it occurs practically to the north bank of the Rio Grande from Laredo to Del Rio, *melacis* itself may inhabit the northern fringes of Coahuila, Nuevo Leon, and/or Tamaulipas states in a manner similar to *Abacion texense* (Loomis) in the order Callipodida (Shelley 1984a). However, this watercourse could be a barrier, with a new species on the southern side. Since the family crosses several large US rivers, including the Mississippi, it may also traverse the Rio Grande, thereby occurring in northeastern Mexico and possibly farther south. Indeed, a new species group or lineage with several components may occur in Mexico, which may provide clues to the relationships of the family.

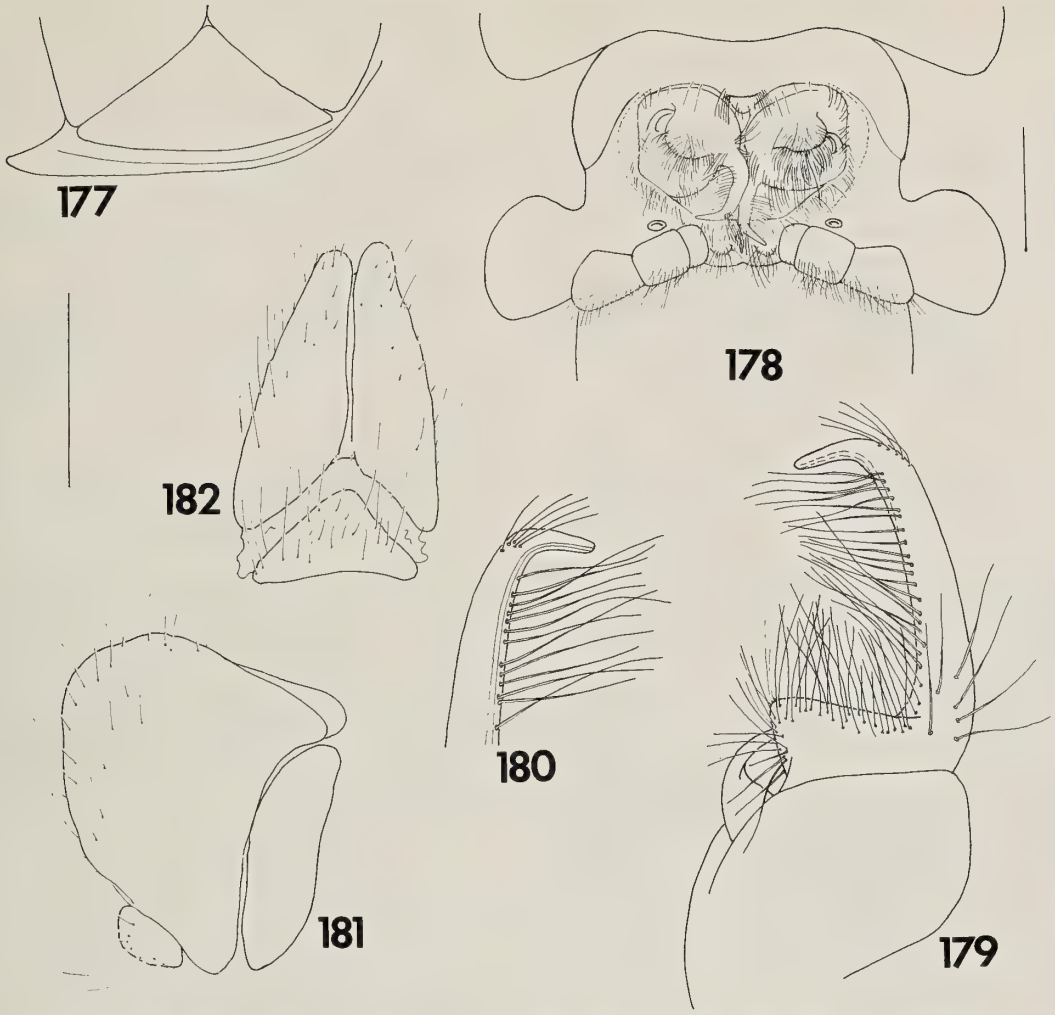
The *melacis* lineage is comprised of one species group, the *melacis* group, and five species.

Components. — *melacis* Chamberlin and Mulaik; *sanbernardiensis* Causey; *digitatus* Loomis; *dactylocyphus,* new species; *clavatus,* new species.

Eurymerodesmus melacis Chamberlin and Mulaik
Figs. 176-182, 212

Eurymerodesmus melacis Chamberlin and Mulaik, 1941:59-60. Chamberlin, 1952:573. Chamberlin and Hoffman, 1958:80. Loomis, 1959:161.

Type specimens. — Male holotype and 57 male, 20 female, and 12 juvenile paratypes (NMNH) collected by S. and D. Mulaik in December 1939 at Edinburg, Hidalgo Co., TX. Other paratypes, all taken by same collectors from localities in Texas and in the NMNH, as follows: Kerr Co., Raven Ranch, ca. 12 mi. S Kerrville, 4F, August 1939, and 22M, 2F, 3 juvs., December 1939; Kendall Co., locality unknown, 9M, 15F, December 1939, and Boerne, 6M, 2F, December 1939; and Bandera Co., locality unknown, 9M, F, December 1939, and 7 mi. N Medina, M, date unknown. The original description does not mention the holotype, and Chamberlin and Hoffman (1958) cited Raven Ranch, Kerr County, as the type locality. In the 11 vials of types, both a male from Edinburg and a female from Raven Ranch are labeled "holotype." Since the former is a male, I regard it as the holotype. A large series was taken from Edinburg at the same time as the



Figs. 177-182. *Eurymerodesmus melacis*. 177, projection of left mandible of holotype, lateral view. 178, aperture and gonopods *in situ* of paratype from Kerr Co., TX, ventral view. 179, left gonopod of holotype, lateral view. 180, telopodite of the same, medial view. 181, left cyphopod of female paratype from Hidalgo Co., TX, caudal view. 182, the same, medial view. Scale lines for fig. 178 = 1.00 mm. Line for other figs. = 0.25 mm for 177, and 0.50 mm for 179-182.

holotype, and the other specimens are properly considered paratypes. Chamberlin and Mulaik (1941) gave no reason for designating so many additional paratypes from other localities, which contrasts markedly with other species of *Eurymerodesmus* authored by Chamberlin where few paratypes were designated.

Diagnosis. — A small species; males characterized by moderate-size mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, with or without slight but continuous elevation with slight suggestion of lobe at caudolateral corners, descending to metazonal surface on caudal margin; telopodite short, usually only slightly overlapping caudal margin; acropodite, short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, bending strongly laterad; prefemur with many hairs arranged continuously along inner surface; cyphopod valves of females not modified, distal corners not produced; receptacle moderate-size, sides not curving round operculum.

Color in life. — Peritremata brick red; dorsum black, metaterga with variably broad, brick red to orange stripes along caudal margins connecting concolorous peritrematal markings; collum with brick red to orange stripes along anterior and caudal margins. These are the colors I noted while collecting *melacis* in 1986. They correspond to Chamberlin and Mulaik's description (1941), who noted that the stripe expands along the midline.

Holotype. — Body highly fragmented, length unmeasurable, maximum width 3.2 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.4 mm, interantennal isthmus 0.8 mm. Antennae reaching back to just beyond 2nd tergite, relative lengths of antennomeres 4>2>3>5>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, clypeal about 10-10, labral about 14-14. Process of mandibular stipes moderate-size, curving slightly inward, narrowly rounded apically (Fig. 177).

Collum extending slightly below ends of following tergite. Paranota depressed, continuing slope of dorsum; posterior corners rounded through segment 7, blunt on 8-12, becoming progressively more acute caudally.

5th sternum with low, rounded lobes between both leg pairs, caudal ones higher; 6th sternum with slightly longer lobes between anterior legs and strong, densely hirsute projections between 7th legs. Postgonopodal sterna with rounded, widely separated knobs between 9th legs; remaining sterna becoming progressively flatter and more plate-like caudally, with variable transverse grooves originating between leg pairs and hair patches adjacent to coxae, latter becoming progressively sparser caudally. 2nd coxa with minute anterior projection, caudal lobe absent. Prefemoral lobes extending through segment 15.

Gonopodal aperture (Fig. 178, not this specimen), broadly trapezoidal, without caudolateral pouches, with moderate-size anterior indentation, 1.6 mm wide and 0.8 mm long at maxima; anterior indentation broadly triangular, apically rounded; sides not divided, nearly straight, leaning slightly over opening, becoming slightly but progressively more elevated caudad, rims essentially smooth; caudolateral corner sharp, distinct, obtuse; caudal margin continuous with sides through caudolateral corner, angling strongly caudomediad, level for part of length with slight suggestion of rounded elevation, then tapering to metazonal surface and continuing flush with latter across midline; margins irregularly hirsute with long hairs arising from rim or short distance down outer surfaces of sides and overhanging opening, with tufts on sides of anterior indentation, lateral hairs becoming thicker caudally, densest on rounded part beyond caudolateral corner, diminishing medially. Gonopods *in situ* (Fig. 178, not this specimen) with telopodites crossing or overlying each other in midline, extending slightly beyond caudal margin of aperture and terminating above sternum between 8th legs, apices bent laterad. Gonopod structure as follows (Figs. 179-180): Telopodite short, terminating well before level of distal extremities of hairs. Prefemur proportionately long, about 3/4 of telopodite length, leaning slightly over coxa, with a continuous row of widely but regularly spaced hairs along inner surface and distomedial tuft of about 5 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, bending strongly laterad, sides tapering continuously to blunt tip.

Male paratypes. — The male paratypes are all tightly coiled, and it is impossible to unroll and straighten most for measurement without breakage. Many shatter, rendering even length approximations impossible. The smaller specimens are more flexible and give the best measurements, but even they usually split between two pregonopodal segments. Approximate measurements on three specimens are length 22.5 mm long, 3.2 mm wide, W/L ratio 14.2%; 18.0 mm long, 3.5 mm wide, W/L ratio 19.4%; and 14.0 mm long, 2.1 mm wide, W/L ratio 1.50%.

The elevation of the sides of the Edinburg males varies, some being nearly flush with the metazonal surface. The caudolateral corner varies, some being nearly flush with the metazonal surface. The caudolateral corner varies from obtuse to squared, or about a right angle, and the most significant differences concern the length of the elevation along the caudal margin and the abruptness of the slope to the metazonal surface. In a few males the elevation stops abruptly at the caudolateral corner, whereas it extends nearly to the midline with a long, gradual slope in others. The rim of the elevation is darkened in most males, and the opening extends significantly caudad in the midline in a few. In all specimens, the elevated part of the caudal margin is level with that of the sides, although males with longer elevations display a suggestion of a slightly higher rounded area just behind the caudolateral corners.

Paratypes from Kerr, Bandera, and Kendall counties closely resemble those from Edinburg. The sides are more linear in some and do not lean over the opening, and the rim is flared outward in a few.

Female paratypes. — An unbroken specimen from Edinburg measures 18.2 mm long, 3.0 mm maximum width, W/L ratio 16.5%. Agreeing essentially with males in somatic features, with following exceptions: interantennal setae 1-1, frontal 1-1. Mandibular stipes with minute projection, acuminate. Sterna flat and unmodified, glabrous.

Cyphopodal aperture elliptical, margins flush with metazonal surface. Cyphopods *in situ* with edges of valves visible in aperture, receptacle hidden under lateral margin. Valves (Figs. 181-182) oriented transversely in aperture, anterior valve slightly larger with rounded corner, moderate-size, extending dorsad on open side, distal margins not produced. Receptacle moderate-size, glabrous, located laterad to valves, sides not curving around operculum. Latter relatively large, clearly visible below open, dorsal, side of valves.

Variation. — *Eurymerodesmus melacis* is a brightly colored species with brick-red peritremata and metatergal stripes through most of the range and a mottled black base color. As noted by Chamberlin and Mulaik (1941) the stripes may be of uniform width or broader in the midline. In the western range periphery, colors assume more of an orange hue, becoming reddish-orange in Kinney County and orange in Tom Green County. The specimens I collected in the latter were so broadly striped and the pigment was so intense that they appeared entirely orange from a distance; actually the metaterga were almost entirely orange with the prozonum mottled black. Chamberlin and Mulaik (1941) described the antennae as pale with the ultimate and distal half of the penultimate articles black. I did not observe this pattern, and the antennae, as well as the genae and clypeus of the Kinney County specimens, were uniformly pale. These individuals exhibited mottled brown pigmentation on the frons, epicranium, and interantennal regions, as opposed to black on the segments, and the mandibular stipes were a lighter mottled brown. Chamberlin and Mulaik (1941) described the venter, sides, and legs as yellowish in the type specimens. The venter was white on the Kinney County individuals, and the legs possessed

brown flecks on the dorsal surfaces, extending onto the sides.

Because they were so tightly coiled and therefore broke or shattered with handling, measurements were impossible on most specimens of both sexes. A few recent molts had not fully hardened and were pliable.

Table 7. Size variation in *E. melacis*.

	Males			Females		
County	Length	Width	W/L	Length	Width	W/L
San Patricio	26.7	3.6	13.5%			
Terrell	17.1	2.6	15.2%			
Medina	25.1	3.7	14.7%	23.1	3.8	16.4%
Medina	21.2	3.0	14.1%	22.6	3.6	15.9%
Medina	21.8	3.3	15.1%	21.9	2.8	12.7%
Medina	23.2	3.8	16.4%	20.5	2.7	13.2%
Medina	21.8	2.9	14.3%	20.3	2.9	14.3%

Aperture variation is as discussed for paratypes. The telopodites appear slightly longer and narrower in scattered individuals, and the distances they extend caudad also vary depending upon how tightly the animal is coiled and how tightly the segments are compressed. In some the anterior half of the aperture is covered by the 6th segment. The lobes between the caudal legs on segment 6 are sharply conical in many individuals from Bexar and Jim Wells counties, being either subequal to or longer than the widths of the adjacent coxae. The process of the mandibular stipes is also quite broad in specimens from Karnes and Frio counties.

The Terrell County male, collected in a cave at the western periphery of the species and family, is by far the smallest adult male of *melacis* and the only one totally pallid, with no evidence of pigmentation. All other cave specimens show evidence of the striped color pattern even after years in preservative. The telopodites are also much shorter in this specimens and the acropodites are more linear and not bent as strongly laterad. Additionally, this male was flexible and easily unrolled for measurement; perhaps it is somewhat cave adapted.

The cyphopod valves are mostly uniform, being squared in profile with rounded corners. In the female from Helotes, Bexar County, the distal corners curve into short rounded lobes, and the corners are also slightly produced and rounded in one from Tom Green County.

Ecology. — In February 1986 *melacis* was common under small branches and shallow leaf layers in small oak thickets at the Welder Wildlife Refuge, San Patricio County. In Tom Green County, I found three specimens under large logs beside the Concho River. Perhaps because of the unseasonable drought, I did not find *melacis* in the lush and ostensively desirable bottomland forests along the Rio Grande in Cameron and Hidalgo counties, but it may be a desertine species actually preferring arid conditions. Thus, these forests may be unsuitable for *melacis,* but it should occur away from this habitat in drier, "inland" areas of Cameron, Hidalgo, and other south Texas counties. Notations on labels with preserved samples are as follows: under rocks (Frio, Kerr, and Uvalde cos.), under cow dung (Bee and Live Oak cos.), under logs (Wilson and Atascosa cos.), and under cardboard in "barditch" (Zavala Co.).

Eurymerodesmus melacis has been taken from 11 caves and can probably be anticipated in any cave in the range, where they are accidental inhabitants found primarily in the open on silt in entrance areas. Except for the specimens from Longley Cave, Terrell county, none vary significantly from epigean populations. As suggested by the anatomical differences, these specimens may be true troglobites, since the opening to this cave is situated so as to virtually preclude the accidental entrance of epigean forms (J. Reddell, pers. comm.).

Distribution. — The Gulf Coastal Plain and eastern Edwards Plateau of central and southern Texas as far west as eastern Terrell County, extending northward from the Rio Grande along the Gulf of Mexico to about the San Antonio River, and inland as far north as southern Hays and western Taylor counties (Fig. 176). Collections are concentrated along an arc running from Corpus Christi to San Antonio to Del Rio, and *melacis* appears rare in south Texas, perhaps an artifact reflecting sampling along major highways before the interstate era. Thus, I shade or outline all of south Texas in figures 1 and 213-214. Specimens were examined as follows:

TEXAS: *Taylor Co.,* 25 mi. SW Abilene, M, March 1944, H. S. Dybas (FMNH). *Tom Green Co.,* 17 mi. NW San Angelo, Wardlaw Ranch, M, F, 26 April 1967 and F, 27 November 1967, G. Brown (FSCA); and San Angelo, along Rio Concho, 2M, F, 27 February 1986, R. M. Shelley (NCSM). *Concho Co.,* 10 mi. W Eden, F, 15 December 1939, collector unknown (NMNH). *Kimble Co.,* Junction, M, 8 March 1986, R. W. Sites (NCSM); 4 mi. SW Junction, M, 24 March 1978, O. F. Francke, T. B. Hall, J. V. Moody (NCSM); and 13 mi. SW Junction, M, 2F, 24 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM). *Terrell Co.,* Longley Cave W of Pandale (Val Verde Co.), M, F, 27 June 1963, J. Reddell (FSCA). *Val Verde Co.,*

near Eliott Spider Cv., 8 mi. N Comstock, Marshall Ranch, M, 1 January 1965, J. Reddell (FSCA); and Del Rio, F. 9 October 1932, O. F. Cook (FSCA). *Edwards Co.,* 11 mi. NE Rock Springs, M, 24 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM). *Kinney Co.,* 21 mi. N Brackettville, 6M, 12 January 1985, S. A. Stockwell and J. M. Steller (NCSM). *Real Co.,* 13 mi. N Leakey, M, 23 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM); and Rio Frio, Prade Ranch, M, F, 21 April 1962, R. O. Albert (FSCA). *Uvalde Co.,* 26 mi. NW Uvalde, F. 12 September 1940, S. and D. Mulaik (NMNH); Laguna, 2M, 25 December 1941, collector unknown (AMNH); 12 mi. NW Uvalde, 5M, F, 23 March 1978, O. F. Francke, T. B. Hall, and J.V. Moody (NCSM); Knippa, M, F, 7 April 1937, K. P. Schmidt (FMNH); Sabinal, 2M, 2F, 4 juvs., 11 January 1933, H. C. McNamara (FSCA); Secret Valley Cv., exact location unknown, M, February 1984, R. M. Waters (NCSM); Tampke Ranch Cv., 0.8 mi. NE Uvalde, 2M, 11 February 1966, J. Reddell and D. McKenzie (FSCA); and Cedar Brake Cv., 25 mi. NE Uvalde, M, 25 October 1965, J. Reddell (FSCA). *Zavala Co.,* 1 mi. E Batesville, 16M, F, 15 March 1982, J. C. Cokendolpher (FSCA). *Kerr Co.,* Raven Ranch, ca. 12 mi. S Kerrville, off TX hwy. 173 north of Camp Verde, 4F, August 1939, 25M, 2F, 3 juvs., December 1939; 4F, juv. June-August 1940; and juv., June 1941, all by S. and D. Mulaik (NMNH); 14 mi. S Kerrvilie, 4M, 2F, 9 October 1976. J. C. Cokendolpher (MSU); and Seven Room Cv., 8 mi. SW Kerrville, 2 juvs., January 1966, J. Fish and J. Reddell (FSCA). *Bandera Co.,* locality unknown, 9M, F, December 1939, S. and D. Mulaik (NMNH); 7 mi. N Medina, M, date unknown, S. and D. Mulaik (NMNH); and Bandera, Shaw Ranch, 4M, 2 February 1962, G. Marion (FSCA). *Medina Co.,* 3 mi. ENE Mico, F. 19 March, year unknown, V. Roth (NCSM); D'Hanis, 13M, 16F, 3 juvs., 18 October 1932, O. F. Cook (NMNH); Windmill Cv., exact location unknown, M, 10 November 1984, S. J. Hardin and J. L. Ivy (NCSM); Koch Cv., 9 mi. N Hondo, M, 7 October 1963, J. Reddell and D. McKenzie (FSCA); and Boehme's Cv., exact location unknown, 19 December 1984, J. L. Ivy (TMM). *Frio Co.,* Pearsall, 2M, 4 February 1961, D. R. Whitehead (RLH). *Kendall Co.,* locality unknown, 9M, 15F, December 1939, S. and D. Mulaik (NMNH); and Boerne, 2M, 3F, 9 April 1911, W. P. Carr (NMNH) and 6M, 2F, December 1939, S. and D. Mulaik (NMNH). *Hays Co.,* Fern Bank Springs nr. Wimberly, F, 1 April 1961, R. Highton (RLH); San Marcos, F, 22 April 1941, K. P. Schmidt (FMNH); and Swift's Cv., exact location unknown, 26 June 1982, D. L. Pate (TMM). *Comal Co.,* between Startzville and Tom Cr., ca. 12 mi. NW New Braunfels, 2F, 15 March 1983, C. S. Lieb (NCSM); Brehmmer Cv., ca. 5 mi. W New Braunfels, F, 19 March 1960, W. J. Gertsch (AMNH); and New Braunfels, F, juv., 29 November 1942, E. S. Ross (CAS), M, 18 December 1954, L. Hubright (RLH), and Landa Park, 4F, 19 June 1964, N. B. Causey (FSCA); and 2 mi. N Bergheim, 2M, 22 February 1986, S. J. Hardin (TMM). *Bexar Co.,* 20 mi. N San Antonio, 5M, 5F, 13 December 1942, E. S. Ross (CAS); Helotes, F, 6 April 1966, D. A. Rossman (FSCA); San Antonio, 2M, F, September, day, year, and collector unknown (MCZ), M, March 1925, A. H. Welolet (NMNH), Yturri Est., 15M, 10F, December 1905, O. F. Cook (NMNH), San Antonio R. at Roosevelt Ave., 16M, 12F, 23 October 1954, L. Hubricht (RLH), and Jessamine St., 11M, 3F, 31 October 1959, J. C. Loomis (RLH); 6 mi. S San Antonio, 4M, 2F, 7 December 1965, T. Stewart (FSCA); Camp Bullis, 15 mi. NW San Antonio, 2M, F, 27 January 1952, H. R. Bullock (AMNH) and 2M, F, 24 April 1966, B. Russell and D. McKenzie (FSCA); Black Cat Cv., 15 mi. NNE San Antonio, M, 2 December 1984, S. J. Harden and J. L. Ivy (NCSM); and Intermittant Spgs. nr. Leon Spgs., F, 3 November 1986, S. J. Harden and C. Lindblom (TMM). *Wilson Co.,* 4 mi. SE Poth, along Marcelinas Cr., M, 2F, 1 April 1961, J. F. Quinlan (FSCA); and 3 mi. W Falls City (in Karnes Co.), F, date and collector unknown (FSCA). *Atascosa Co.,* Campbellton, M, FF, 15 May 1961, J. F. Quinlan (FSCA). *Karnes Co.,* 1 mi. NW Falls City, M, 3F, 9 April 1961, J. F. Quinlan (FSCA); Falls City, M, F, 29 October 1961, J. F. Quinlan (FSCA); and Karnes City, 2M, 4F, 14 November 1959, N. B. Causey (FSCA). *Golida Co.,* Goliad St. Pk., 3F, 17 April 1955, L. Hubright (RLH). *Bee Co.,* Beeville, F, 11 November 1895, collector unknown (NMNH) and M, 28 December 1941, R. Perita (AMNH). *Live Oak Co.,* Largato, 2M, 2F, 18 February 1961, R. O. Albert (FSCA); 6 mi. SE Whitsett, 3M, 11 December 1984, R. S. Zack (WASU); and George West, 2M, 6F, 3 December 1960, collector unknown (FSCA). *Refugio Co.,* along Aransas R., F, May 1952, collector unknown (FSCA). *San Patricio Co.,* 7 mi. N Sinton, Welder Wildlife Ref., 40M, 26F, 8 juvs., February and December 1961, December 1965, and November 1970, R. O. Albert (FSCA), F, 18 October 1967, C. Parrish (CAS), and 8M, 5 juvs., 21 February 1986, R. M. Shelley (NCSM); and 4-5 mi. SW Mathis, 9M,

9F, 3 juvs., March 1961 and January 1962, R. O. Albert (FSCA). *Jim Wells Co.,* along Nueces R., 10M, 6F, 1-3 April 1962, R. O. Albert (FSCA). *Duval Co.,* unknown locality in NE corner, 2M, 2F, 4 April 1962, R. O. Albert (FSCA); San Diego, 9M, F, 8 January 1961, R. O. Albert (FSCA); and 5 mi. S San Diego, M, 2F, 17 February 1961, R. O. Albert (FSCA). *Hidalgo Co.,* Edinburg, 57M, 21F, 12 juvs., December 1939, S. and D. Mulaik (NMNH) TYPE LOCALITY.

Additional literature records for *melacis* deemed valid include McQueeney and Schertz, Guadalupe County (Loomis 1959).

Remarks. — Hoffman (1981) noted that some published Edinburg spider records are patently mislabeled, and since that for *melacis* is around 100 miles south of the closest known locality, in Duval County, the question as to whether it too may be erroneous assumes considerable importance, since Edinburg is now the type locality. The aforementioned absence of *melacis* from the forests of the Rio Grande Valley in contrast to its abundance in small thickets in San Patricio County is not troubling because *melacis* does not seem to be a forest-inhabiting species. The site where I collected it along the Rio Concho in San Angelo, Tom Green County, was grassland with a few widely scattered trees and no leaf litter, which I think reflects its habitat preferences. Since Edinburg is away from these woodlands, it is an ecologically plausible site for *melacis.* That no specimens have been collected in other counties in the tip of Texas, particularly intervening ones like Brooks and Jim Hoff, I think reflects their relative isolation. There are few towns or places to look for millipeds, and collectors passing through may have set their sights on the Rio Grande forests instead of the arid grasslands away from the river. Edinburg is not so far removed from other known sites as to be implausible, and there could also be an allopatric population there analogous to those of *b. birdi* in San Patricio, Wilson, Bastrop, and Bell counties. Thus, although confirmation with fresh material is desirable, Edinburg is a logical site for *melacis.*

As the southernmost species known essentially to the Rio Grande in Webb, Kinney, and Val Verde counties, *melacis* may be analogous to *Abacion texense* and occur south of the border in northern parts of Tamaulipas, Nuevo Leon, and/or Coahuila provinces, Mexico (Shelley 1984a). Mexican and American biologists working in these areas should be alert for this small, bright red milliped.

Eurymerodesmus melacis is also the westernmost eurymerodesmid, and its occurrence on the eastern Edwards Plateau in central Texas suggests occurrence farther west in the Davis Mountains, the Permian Basin, the panhandle around Lubbock, and possibly even the southeastern corner of New Mexico. I therefore spent a week in February 1986 searching for it around Lubbock and in the Davis Mountains, with no success. I searched habitats similar to those in which I found it at San Angelo and the Welder Wildlife Refuge, but the only millipeds encountered were parajulids. Future discoveries are always possible, but I think the current western limits are close to the actual ones.

Eurymerodesmus dactylocyphus, new species
Figs. 177, 183-189, 212

Type specimens. — Male holotype and two male and three female paratypes (FSCA) collected by R. O. Albert, 1 December 1963, at Maxwell, Caldwell Co., TX. One male and one female paratypes deposited in NCSM.

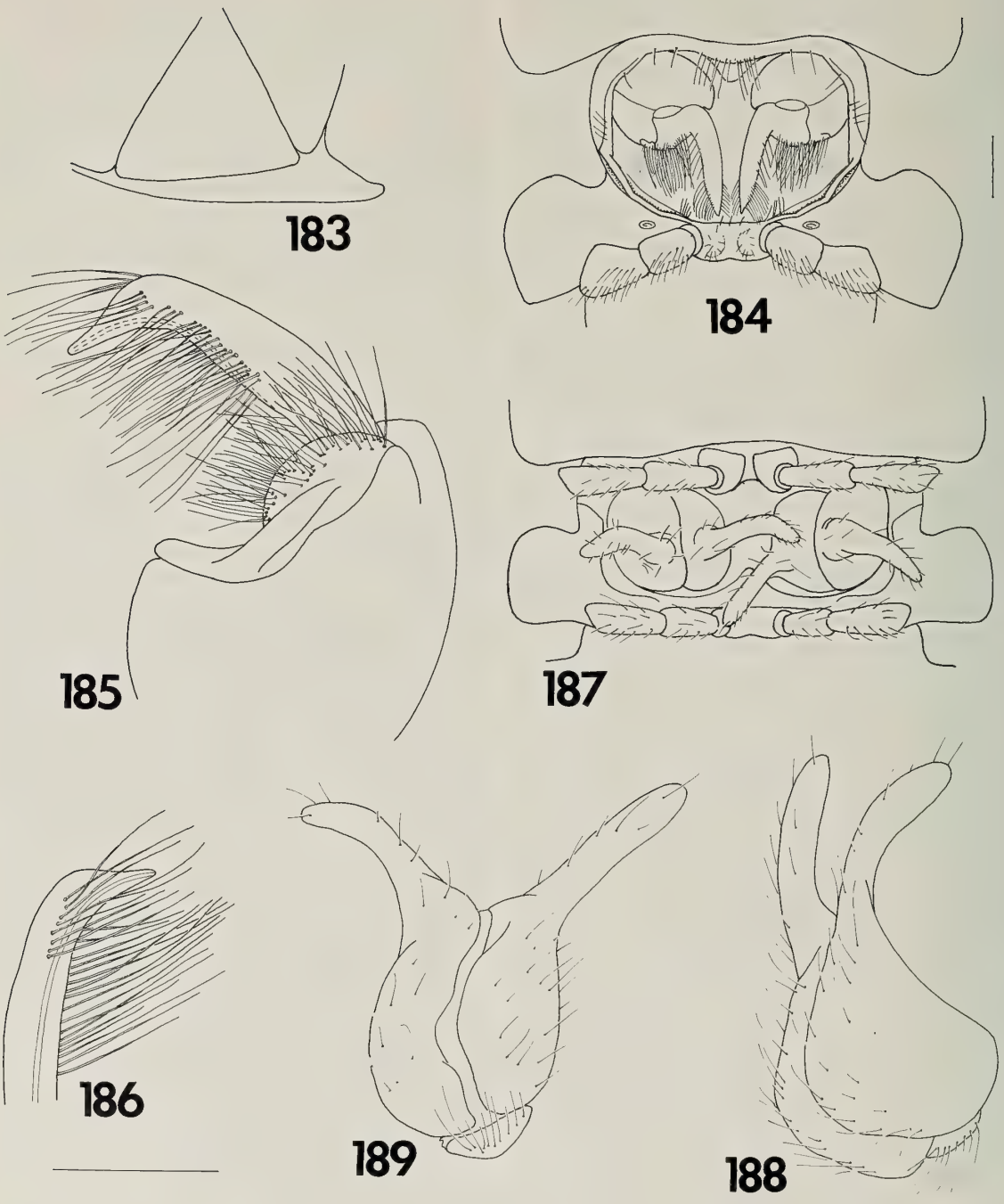
Diagnosis. — A small to moderate-size species; males characterized by long mandibular projection; aperture very large, occupying entire breadth of segment in ventral view; sides not divided, without caudolateral pouches, with variable caudal elevation continuing around caudolateral corners ranging from slight rise to long flange; caudal margin descending rapidly to metazonal surface; telopodite short, wholly enclosed within aperture; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, bending directly dorsad; cyphopod valves of females with distal corners of valves produced into variable projections, ranging from small nubbinlike tubercles to long, flexible dactyliform projections, extending well beyond cypopodal aperture and overlapping succeeding two segments *in situ;* receptacle small, submerged in valves, sides not curving around operculum.

Color in Life. — Unknown.

Holotype. — Length 19.7 mm, maximum width 3.0 mm, W/L Ratio 15.2%.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 1.8 mm, interantennal isthmus 0.6 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>6>4>5>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, and genal absent, subantennal 1-1, frontal 1-1, clypeal about 10-10, labral about 14-14. Process of mandibular stipes relatively long, subtriangular, narrowly rounded apically (Fig. 183).



Figs. 183-189. *Eurymerodesmus dactylocyphus.* 183, projection of right mandible of holotype, lateral view. 184, aperture and gonopods *in situ* of holotype, ventral view. 185, left gonopod of the same, lateral view. 186, telopodite of the same, medial view. 187, cyphopods *in situ,* ventral view of female paratype. 188, left cyphopod of the same, medial view. 189, the same, anterior view. Scale lines for figs. 184 and 187 = 1.00 mm. Line for other figs. = 0.30 mm for 183 and 188-189, and 0.50 mm for 185-186.

Collum extending slightly below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, peritremata somewhat flattened; posterior corners rounded through segment 9, blunt on 10-12, becoming progressively more acute posteriorly.

5th sternum with small paramedian lobes between leg pairs; 6th sternum with broader, higher elevated areas. Postgonopodal sterna with low paramedian knobs between 9th legs; remaining sterna becoming progressively flatter, more plate-like, and less hirsute caudally, with variably distinct transverse grooves between pairs and broad central depressions, hairs diminishing after segment 9. 2nd coxa with large, rounded anterior and posterior lobes. Prefemoral lobes extending through segment 10.

Gonopodal aperture (Fig. 184) very large, nearly circular but broadly ovoid, without caudolateral pouches, with strong anterior indentation, 1.9 mm wide and 1.0 mm long at maxima, extending nearly to anterior edge of segment; anterior margin slightly elevated, in form of narrow rim continuing around anterolateral corners onto sides, anterior indentation broad, apically rounded; sides not divided, indented slightly and elevated at anterolateral corner, then linear for short distance, caudal half angling mediad, anterior half continuous with elevated anterior margin, elevation increasing rapidly and dramatically just beyond midlength, extending into long, broad, ventrally directed flange at caudolateral corners, rims mostly smooth, becoming slightly irregular on flange; caudolateral corners slightly angular, greatly elevated; caudal margin continuous with caudal elevation of sides, flange narrow, inner surface curved or cupulate, very long, extending nearly to midlength of podomeres, terminating abruptly a short distance beyond corner, margin low medially, curving across midline and merging with lobes between 9th legs; margins irregularly hirsute, with tufts of three to four hairs on anterior indentation, scattered hairs on rim of anterolateral corners and sides, a few arising from inner surfaces of flanges, and three to four on low, central part of caudal margin. Gonopods *in situ* (Fig. 184) with telopodites extending nearly directly caudad, angling slightly mediad, terminating short of caudal margin, wholly enclosed by aperture, apices directed dorsad. Gonopod structure as follows (Figs. 185-186): Telopodite relatively short, terminating well before level of distal extremities of hairs. Prefemur proportionally long, about 3/4 of telopodite length, leaning over coxa, broad basally, tapering slightly distad, with three rows of continuous, dense, regularly spaced hairs along inner margin and distomedial tuft of 8 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, continuing distal curvature of latter, curving dorsad, sides narrowing rapidly to subacuminate tip.

Male paratypes. — The male paratypes agree with the holotype in all particulars.

Female paratype. — Length 22.1 mm, maximum width 2.8 mm, W/L ratio 12.7%. Agreeing essentially with males in somatic features, with following exceptions: Mandibular stipes with corner slightly produced, blunt. Sterna flat and unmodified, glabrous.

Cyphopodal aperture large, rectangular, caudal margin slightly elevated above metazonal surface, indented slightly anteriad in midline. Cyphopods *in situ* (Fig. 187) with valves oriented along body axis, protruding slightly through opening, dactyliform projections extending well beyond aperture and overlapping legs of segments 3 and 4, directed either ventrad or laterad, appearing like supernumerary legs. Valves (Figs. 188-189) large, unequal, lateral one larger, distal corners extending into long, flexible, widely separated dactyliform projections, subequal to or longer than valves proper, projecting directly ventrad basally, curving caudad at midlength, apically blunt. Receptacle small and inconspicuous, located on caudal side of, and submerged in, valves. Operculum small, located under anterior corner of valves.

Variation. — As described for the holotype, males from Hays County exhibit large, cupped aperture flanges, which drop nearly perpendicularly to the metazonal surface on the caudal margin just beyond the caudolateral corner. However, in Bell, Bosque, and Victoria counties the elevation is only slightly higher than the metazonal surface. The paramedian sternal projections between the 9th legs, very large and coalesced in the Victoria males, are subequal to the widths of the adjacent coxae, which have hirsute ventrodistal lobes. In Bell County, the 9th sternal knobs are separate. On the gonopods, the prefemur tapers distad in the Hays County males and possesses a slight shoulder on the outer margin; thus, the acropodite is more strongly demarcated from the prefemur. In Bell County, the acropodite curves strongly dorsad.

The longest dactyliform cyphopodal projections occur in females from Hays and Caldwell counties. They are shorter, more variable, and more unequal in those from Bosque and Victoria counties. In the latter, the projections vary from small nubbinlike tubercles or papillae to digitiform elongations about half as long as the valves. Both conditions can occur on a single cyphopod.

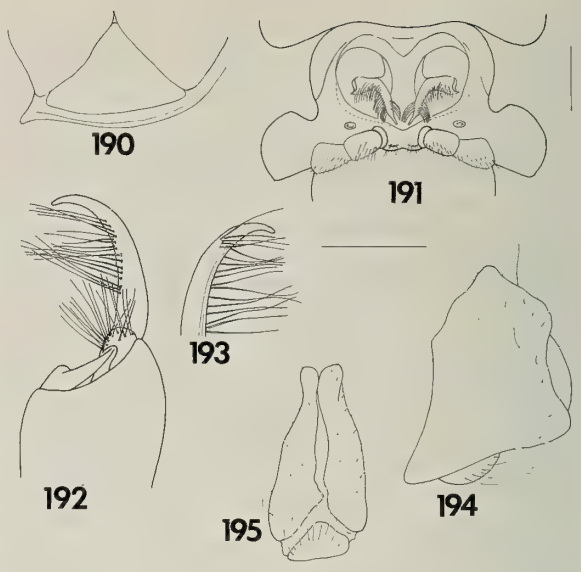
Ecology. — Some of the Victoria specimens were encountered in sedge-grass roots in a sandy region and on a shaded river bank. A male from Bell County was collected along a fence.

Distribution. — The eastern fringe of the Central Plains to the Gulf of Mexico between the Brazos and Guadalupe Rivers (Figs. 176, 212). Specimens were examined as follows:

TEXAS: *Bosque Co.,* Meridian St. Pk., 5M, 26 December 1979, G. Spicer (NCSM) and 2M, 2F, 5 October 1980, G. Spicer (NCSM). *Bell Co.,* Belton, M, January 1931, collector unknown (NMNH); and 1 mi. W Belton, 2M, 24 December 1939 and 1941, collector unknown (AMNH). *Williamson Co.,* Three Mile Cv., ca. 3 mi. W Round Rock, M, 1 December 1962, R. O. Albert (TMM). *Hays Co.,* Fern Bank Springs nr. Wimberly, 2M, 1 April 1961, R. Highton (RLH); and San Marcos, F, 22 April 1941, K. P. Schmidt (FMNH). *Caldwell Co.,* Maxwell, 4M, 4F, 1 December 1963, R. O. Albert (FSCA) TYPE LOCALITY. *Victoria Co.,* Victoria, 50 M, 35 F, 7 juvs., December 1905, August 1906, 23 November 1911, 24 November 1912, 10 March 1913, and 11 December 1915, J. D. Mitchell (NMNH).

Remarks. — A female of *melacis* was found in the samples from Wimberly and San Marcos, suggesting that their ranges abut in southern Hays County. The male from Belton was retrieved from a sample of *b. birdi,* suggesting that the two species are sympatric in Bell County.

The gonopods of *dactylocyphus* appear ridiculously small in contrast to the enormous aperture. In some males the coxa is tucked under the anterior margin and appears swallowed by the aperture, which is mostly empty and thus filled with debris. The species has by far the broadest aperture in the genus, filling essentially the breadth of the metazonum in ventral view and extending laterad nearly to the level of the paranota. In some males, it compresses the prozonum into a remnant, an extremely narrow sliver, along the anterior segmental margin, the minimum necessary to give form to the aperture and hold it together. This is a striking feature of males, but I found the cyphopod projections equally sensational and decided to name the species for this distinctive aspect of females. These projections vary greatly, as described above, and the long ones are convergent with those in *compressus.* However, the projections in *dactylocyphus* differ in being flexible, as opposed to stiff and rigid. The projections are foreshortened in figure 187, appearing shorter than they really are, fully as long as the next two segments combined. In some females they project outward between the appendages of the following segment, thus appearing at first glance as additional legs, when seen in lateral view.



Figs. 190-195. *Eurymerodesmus sanbernardiensis.* 190, projection of left mandible of male from Colorado Co., TX, lateral view. 191, aperture and gonopods *in situ* of the same, ventral view. 192, left gonopod of the same, lateral view. 193, telopodite of the same, medial view. 194, left cyphopod of female from Colorado Co., lateral view. 195, the same, anterolateral view. Scale line for fig. 191 = 1.00 mm. Line for other figs. = 0.40 mm for 190 and 195, and 0.50 mm for 192-194.

Eurymerodesmus sanbernardiensis Causey
Figs. 176, 190-195, 212

Eurymerodesmus sanbernardiensis Causey, 1952a:174, figs. 6-7. Chamberlin and Hoffman, 1958:81.

Type specimen. — Female holotype (ANSP) collected by N. B. Causey, 3 January 1952, along the San Bernard River near the crossing of US highway 59, Fort Bend Co., TX. The cyphopods and segment 3 are missing from the holotype and their separate vial at the ANSP, and are lost. My attempt to collect topotypes in February 1986 was unsuccessful. Since its cyphopods roughly resemble those in Causey's illustrations (1952a, figs. 6-7), I assign *sanbernardiensis* to the form occurring at Wharton, Wharton County, approximately 12 miles south of the type locality.

Diagnosis. — A small to moderate-size species; males characterized by short, triangular mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, elevating slightly around caudolateral corner, descending to metazonal surface along caudal margin; telopodite short, at most barely overlapping caudal margin of aperture; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, curving broadly dorsad; prefemur with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners produced and rounded; receptacle small, partly submerged in valves, sides not curving around operculum.

Color in life. — Paranota orange; rest of color unknown. Causey (1952a) stated that the dorsum was mottled with orange, but that the color was "not completely developed."

Male from Wharton Co. — Length 22.7 mm, maximum 3.1 mm, W/L ratio 13.7%.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 1.8 mm, interantennal isthmus 0.8 mm. Antennae reaching back to midlength of 3rd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, genal, and frontal absent, clypeal about 11-11, labral about 15-15. Projection of mandibular stipes short, triangular (Fig. 190).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum; posterior corners rounded through segment 8, blunt on 9-13, becoming progressively more acute posteriorly.

5th and 6th sterna with hirsute elevated areas between leg pairs, without lobes. Postgonopodal sterna flattened, plate-like, with variably complete transverse grooves originating between leg pairs on all segments and variably broad central depressions, with hair patches adjacent to leg coxae becoming sparser caudally. 2nd coxa with minute anterior swelling, without caudal lobe or swelling. Prefemoral lobes terminating on 12th legs.

Gonopodal aperture (Fig. 191, not this specimen) broadly ovoid, without caudolateral pouches, with broad anterior indentation, 1.2 mm wide and 0.8 mm long at maxima; anterior indentation moderately long, broadly triangular, apically acuminate; sides curving broadly, undivided, not leaning over opening, anterior half flush with metazonal surface, elevating at midlength and becoming slightly and progressively higher to caudolateral corner, rims essentially smooth; caudolateral corner obtuse, indistinct; caudal margin continuous with sides at caudolateral corner, tapering gradually to metazonal surface, extending slightly caudad in midline; margins glabrous. Gonopods *in situ* (Fig. 191, not this specimen) with telopodites angling caudomediad, terminating before level of caudal aperture margin, apices directed dorsad. Gonopod structure as follows (Figs. 192-193): Telopodite short, terminating well before level of distal extremities of hairs. Prefemur proportionally long, about 3/4 of telopodite length, curving over coxa, curve increasing distad, moderately broad basally, sides tapering distad, with two rows of continuous, regularly spaced hairs on inner surface and distomedial tuft of 5-6 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, continuing broad dorsal curvature of prefemur, sides tapering to subacuminate tip.

Female from Wharton Co. — Length 21.9 mm, maximum width 2.9 mm, W/L ratio 13.2%. Agreeing closely with males in somatic features, with following exceptions: frontal setae 1-1, genal 4-4. Mandibular stipes with short, rounded projection. Sterna flat and unmodified, glabrous.

Cyphopodal aperture elliptical, caudal margin slightly elevated above metazonal surface, indented slightly anteriad at midline. Cyphopods *in situ* with valves oriented obliquely, distal corner protruding through opening. Valves (Figs. 194-195) small, unequal, caudal valve slightly larger, distal corners slightly produced and rounded. Receptacle small, inconspicuous, partly submerged in valves, located below latter on lateral side. Operculum small, located at bases of valves on medial side.

Variation. — The sides of the aperture are a little higher on two of the four males from Wharton County. Depending upon how submerged the coxae are in the aperture, the telopodites may or may not extend beyond the caudal margin and overhang the sternum between the 9th legs *in situ*. Specimens from Brazoria and Colorado counties agree closely with those from Wharton except for a slight bisinuate curvature on the acropodites of those from Colorado County. In these males the structure resembles a tarsal claw, since it is moderately long, similarly curved, and arises from a hirsute prefemur. Females are closely similar throughout the range.

Ecology. — The type locality, which I visited in February 1986 in an unsuccessful search for topotypes, is a narrow bottomland forest that merges into grassland a short distance away from the river. There were plenty of logs, debris, and other potential milliped habitat, but no eurymerodesmids. The female that I collected at Richmond, Fort Bend County, was found under leaves at a rest area near the Brazos River.

Distribution. — A small area of the Gulf Coastal Plain of southeastern Texas between the Brazos and Colorado Rivers, extending from the Gulf of Mexico to about 94 miles inland (Figs. 176, 212). Specimens were examined as follows:

TEXAS: *Austin Co.*, New Ulm, 9M, 6F, 3 February 1963, R. O. Albert (FSCA). *Colorado Co.*, Columbus, 3M, 23 December 1961, C. L. Redus (FSCA). *Fort Bend Co.*, ca. 2 mi. S Kendleton, along US hwy. 59 at San Bernard R., F, 3 January 1952, N. B. Causey (ANSP) TYPE LOCALITY; and Richmond, F, 20 February 1986, R. M. Shelley (NCSM). *Wharton Co.*, Wharton, Bank of Colorado R., 4M, 10F, 4 juvs., December 1905, collector unknown (NMNH). *Brazoria Co.*, Old Ocean and 2.4 mi. S Old Ocean, 2M, juv., 23 December 1961, R. O. Albert (FSCA).

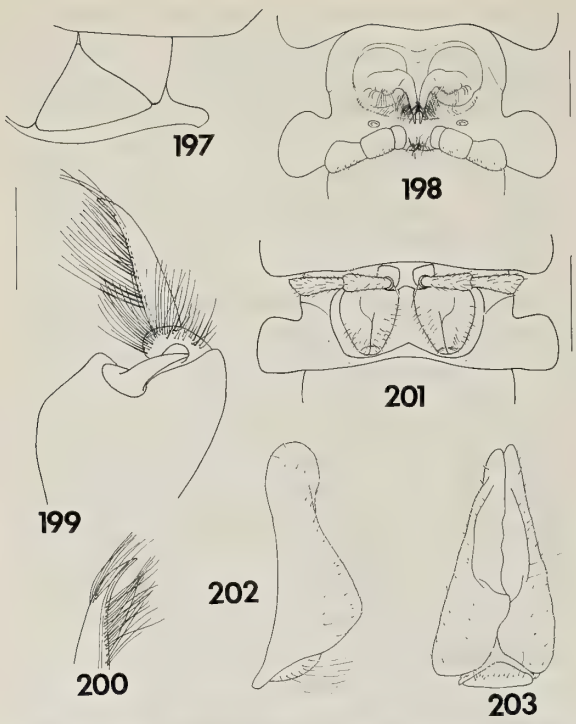
Remarks. — In his key to Texas species of *Eurymerodesmus,* Loomis (1976) stated that the valves of female cyphopods of *sanbernardiensis* are of unequal length. This was probably based on Causey's description (1952a), which I think may have been of an immature female as judged by the size of the holotype versus Wharton females. As redefined here, the valves of *sanbernardiensis* are so nearly equivalent in size that this feature would not distinguish it from Texas congeners.

Eurymerodesmus digitatus Loomis
Figs. 176, 197-203

Eurymerodesmus digitatus Loomis, 1976:288-289, figs. 1-3.

Type specimens. — Male holotype and female allotype (FSCA), and one male and one juvenile paratype (NMNH), collected by J. C. Loomis, 15 February 1975, 5 mi. ESE Marble Falls, Burnet Co., TX.

Diagnosis. — A small to moderate-size species; males characterized by long mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, elevating to various heights around caudolateral corner, descending to metazonal surface at varying distances along caudal



Figs. 197-203. *Eurymerodesmus digitatus.* 197, projection of right mandible of holotype, lateral view. 198, aperture and gonopods *in situ* of paratype, ventral view. 199, left gonopod of the same, lateral view. 200, telopodite of the same, medial view. 201, cyphopods *in situ,* ventral view of female from Llano Co., TX. 202, left cyphopod of allotype, oblique caudal view. 203, the same, oblique anterior view. Scale lines for figs. 198 and 201 = 1.00 mm. Line for other figs. = 0.35 for 1987, 0.40 mm for 202-203, and 0.50 mm for 199-200.

margin; telopodite usually short, usually barely overlapping caudal margin of aperture; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur, curving variably dorsad; prefemur with many hairs arranged continuously along inner margin; cyphopod valves of females usually with distal corners extended, broadly curved; receptacle small, indistinct, submerged in valves, sides not curving around operculum.

Color in Life. — Not known with certainty. Loomis (1976) reported that both the color and pattern were "apparently much as in *melacis,*" but did not describe them *per se.* Thus, *digitatus* probably exhibits red paranota, red caudal metatergal stripes, and red borders on the collum.

Holotype. — Specimen highly fragmented, length unmeasurable, maximum width 2.7 mm.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 2.0 mm, interantennal isthmus 0.9 mm. Antennae reaching back beyond caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, subantennal, and genal absent, frontal 1-1, clypeal about 7-7, labral about 13-13. Process of mandibular stipes long, tip broadly rounded (Fig. 197).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 10, blunt on 11-14, becoming progressively more acute posteriorly.

5th sternum with low, rounded elevated areas between leg pairs, caudal ones larger and more widely separated; 6th sternum with knob-like processes between leg pairs, caudal ones longer and more widely separated. Postgonopodal sterna with distinct knob-like projections between 9th legs, narrowly segregated in midline; remaining sterna becoming progressively flatter and more plate-like posteriorly with progressively sparser hair patches adjacent to leg coxae. 2nd coxa with distinct, subconical anterior lobe and small caudal projection. Prefemoral lobes extending through segment 9.

Gonopodal aperture (Fig. 198, not this specimen) broadly ovoid, without caudolateral pouches, with moderate anterior indentation, 1.7 mm wide and 0.7 mm long at maxima; anterior indentation moderately long, subtriangular, apically rounded; sides not divided, gently curved, leaning slightly over opening, becoming slightly and progressively more elevated caudad, rims essentially smooth; caudolateral corner broad, slightly angled; caudal margin continuous with sides at caudolateral corner, elevation sloping rapidly to metazonal surface and terminating just beyond caudolateral corner, curving gently across midline; margins with only a few hairs arising from rims of elevations at caudolateral corners and adjacent parts of sides and caudal margin. Gonopods *in situ* (Fig. 198, not this specimen) with telopodites extending caudad in parallel arrangement along midline, extending just beyond caudal margin of aperture, tips directed dorsad. Gonopod structure as follows (Figs. 199-200): Telopodite short, terminating well before level of distal extremity of hairs. Prefemur short but proportionally long, about 7/8 of telopodite length, upright for most of length, trace of curvature distad, broad basally, tapering slightly distad, with three rows of continuous, regularly spaced hairs on inner surface and distomedial tuft of about 6 hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, continuous with, and poorly demarcated from, prefemur, continuing slight distal curvature of latter and directed dorsad, sides tapering rapidly to acuminate tip.

Male paratype. — Agreeing closely with holotype in all particulars.

Female allotype. — Fragmented, length unmeasurable, maximum width 2.4 mm. Agreeing essentially with males in somatic features, with following exceptions: Mandibular stipes with short, broadly rounded process. Sterna flat, with progressively sparser hair tufts adjacent to leg coxae on segments 4-7 and an occasional scattered hair thereafter.

Cyphopodal aperture elliptical, sides slightly elevated above metazonal surface. Cyphopods *in situ* (Fig. 201) with valves extending caudad along body axis, distal corners curved, protruding through opening. Valves (Figs. 202-203) moderate-size, subequal, distal corners extended, long, curved, and rounded, sides extending slightly around receptacle. Latter small, located on medial side of valves, submerged in and obscured by latter, invisible from caudal and anterior perspectives. Operculum small, tucked under free, dorsal side of valves.

Variation. — *Eurymerodesmus digitatus* undergoes considerable variation, and forms from Blanco

and Llano counties, adjacent to Burnet County, closely resemble the types. In these individuals, the aperture sides are higher, and in the Blanco County males, the elevation continues around the caudolateral corner for about 1/3 of the length of the caudal margin. The gonopods are very close to the types, but the corners of the cyphopod valves of Llano County females are not as elongate as those of the allotype.

The Travis County males display much wider apertures, and that from Elbow Cave (FSCA) is also much longer, extending nearly to the anterior segmental margin, thereby resembling the condition in *dactylocyphus*. The elevation is higher caudally on the sides, and in that from Elbow Cave, it begins abruptly at midlength on the sides, tapering nearly to the metazonal surface at the caudolateral corner. In one male from along Waller Creek, the sides lean noticeably over the opening, whereas in others from that site, the rim is flared laterad at the caudolateral corner. Except for the Elbow Cave male, the gonopods are very close to the holotype. In this individual the telopodites are longer, the prefemur curves more noticeably dorsad distally, and the acropodite does so even more strongly. Females are unknown from Travis County.

The Tarrant County males also display longer telopodites, extending to the level of the distal extremity of the hairs and farther from the aperture, terminating between the 8th legs. The mandibular process is shorter, broader, and subtriangular, and the cyphopod valves of females are not extended.

The Oklahoma males, found mixed in a sample with *mundus,* display a broader aperture with only slight elevation at the caudolateral corner. The mandibular projection resembles that in Tarrant County males.

Ecology. — Unknown. The vial labels lack indications of habitat, and nothing was mentioned in the original description.

Distribution. — A band along the boundary between the Central and Coastal Plains, extending from southwestern Oklahoma to central Texas near the Pedernales River (Figs. 176, 212). Specimens were examined as follows:

OKLAHOMA: *Comanche Co.,* Mt. Scott, 3M, 25 October 1974, G. Beck (MSU).

TEXAS: *Tarrant Co.,* Fort Worth, Normandy Dr., 20M, 24F, 4 juvs., 3 November 1979, G. Spicer (NCSM). *Burnet Co.,* 5 mi. ESE Marble Falls, 2M, F, juv., 15 February 1975, J. C. Loomis (FSCA, NMNH) TYPE LOCALITY. *Llano Co.,* 13 mi. SE Llano, 4M, 3F, 11 March 1961, J. F. Quinlan (FSCA); and 27.8 mi. N Fredericksburg (Gillespie Co.), jct. TX hwys. 16 and 965, 10M, 13 March 1982, J. C. Cokendolpher (NCSM). *Blanco Co.,* 2 mi. N Johnson City, 2M, 13 March 1982, J. C. Cokendolpher (FSCA). *Travis Co.,* Austin, 4M, 5F, date and collector unknown (NMNH), and 4M, 19 November 1945, collector unknown (NMNH); along Waller Cr., 7M, juv., November 1963, J. Reddell (FSCA) and F, 9 April 1983, J. Reddell (TMM); and Elbow Cave, 3 mi. N Austin, M, February 1963, B. Russell (FSCA).

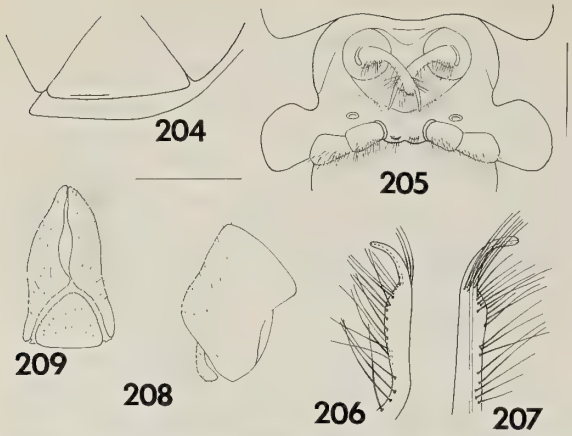
Remarks. — Chamberlin recognized that this form represented a new species and inserted a label stating "*E. austini* Chamb., Types" with the first sample from Austin, Travis County. However, this name was never validated and Loomis (1976) receives authorship credit.

Eurymerodesmus digitatus is similar to *melacis,* but differs in the genitalia of both sexes. The cyphopod valves are not elongate in *melacis,* whereas they are in the most proximate populations of *digitatus* with females. The gonopodal apertures are similar in general configuration, but that of *digitatus* is larger and the lateral elevation is more variable. The telopodites of *melacis* are uniform, and are longer and narrower than those of *digitatus.* The chief difference is the configuration and direction of the acropodite, which bends sharply laterad in *melacis* and curves gently dorsad in *digitatus.* This structure's curvature is slight in all males except that from Elbow Cave, Travis County, where it is stronger.

In contrast to *melacis,* there is little difference between *digitatus* and *sanbernardiensis,* and future collecting in Lee, Bastrop, Fayette, and Williamson counties may show them to be subspecifically related. For now I retain both names and distinguish them by the length and curvature of the acropodite, short and gently curved in *digitatus,* and longer and more strongly curved in *sanbernardiensis.*

Though differing in details of the gonopods, aperture, mandibular projection, and female cyphopods, I do not think that the differences between the populations of *digitatus* are of sufficient magnitude to warrant taxonomic recognition for forms in Travis and Tarrant counties, Texas, and Comanche County, Oklahoma. The last two sites are so widely separated from the type locality that differences could easily be bridged by forms from intervening areas.

As stated previously, the telopodites of *digitatus* are convergent with those of *dubius* as shown by comparing figures 47-48 and 199-200.



Figs. 204-209. *Eurymerodesmus clavatus.* 204, projection of left mandible of paratype, lateral view. 205, aperture and gonopods *in situ* of holotype, ventral view. 206, telopodite of left gonopod of the same, lateral view. 207, the same, medial view. 208, left cyphopod of female paratype, caudal view. 209, the same, medial view. Scale line for fig. 205 = 1.00 mm. Line for other figs. = 0.5 mm for each.

Eurymerodesmus clavatus, new species
Figs. 176, 204-209, 212

Type specimens. — Male holotype and 7 male and 5 female paratypes (FSCA) collected by R. O. Albert, 3 February 1963, at New Ulm, Austin Co., TX. One male and one female paratypes deposited in NCSM.

Diagnosis. — A small species; males characterized by short mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, elevating slightly to caudolateral corners, descending to metazonal surface along caudal margin; telopodite short, barely overlapping caudal margin of aperture; acropodite moderately long, about 1/3 of telopodite length, narrowly terminal, arising solely from outer prefemoral margin; prefemur with many hairs arranged continuously along inner margin, expanding distad into clavate shoulder on inner margin; cyphopod valves of females with distal corners slightly extended; receptacle small, partly submerged in valves, sides not curving around operculum.

Color in Life. — Unknown.

Holotype. — Length 14.1 mm, maximum width 1.6 mm, W/L ratio 11.3%.

Somatic features similar to *hispidipes,* with following exceptions:

Width across genal apices 1.2 mm, interantennal isthmus 0.6 mm. Antennae reaching back to anterior half of 3rd tergite, relative lengths of antennomeres 2>3>6>5>4>1>7. Genae without impressions. Facial setae as follows: epicranial 1-1, interantennal, subantennal, and genal absent, frontal 4-4, clypeal about 9-9, labral about 14-14. Process of mandibular stipes short, subtriangular, apically acute (Fig. 204).

Collum not extending below ends of following tergite. Paranota moderately depressed basally, continuing slope of dorsum, peritremata somewhat flattened; posterior corners blunt on segments 1-3, rounded on 4-7, blunt on 8-13, becoming progressively more acute posteriorly.

5th and 6th sterna with small hirsute areas adjacent to leg coxae but without lobes or projections. Postgonopodal sterna with flattened hirsute areas adjacent to 9th coxae; remaining sterna becoming flatter, more plate-like, and less hirsute caudally. 2nd coxa without lobes, gonapophyses relatively long, extending to near midlength of 4th sternum. Prefemoral lobes small, not pronounced, extending through segment 8.

Gonopodal aperture (Fig. 205) small, heart-shaped, without caudolateral pouches, with moderate anterior indentation, 0.7 mm wide and 0.3 mm long at maxima; anterior indentation moderate-size, broadly triangular, apically rounded; sides not divided, angling strongly mediad, becoming slightly elevated caudad, rims smooth; caudolateral corner poorly defined, indistinct, continuous with lateral curvature; caudal margin continuous with sides, angling to point in midline, slightly elevated and thickened at approximate location of caudolateral corner, flush with segmental surface in midline; margins nearly glabrous, with only 6 or so hairs on thickening at caudolateral corner. Gonopods *in situ* (Fig. 205) with telopodites crossing in midline and extending slightly over opposite side of aperture. Gonopod structure as follows (Figs. 206-207): Telopodite terminating just before level of distal extremities of hairs. Prefemur proportionally short, about 2/3 of telopodite length, upright but with slight bisinuate curve, relatively narrow basally, expanding near midlength and continuing distad into broad shoulder on inner margin, with two rows of continuous, regularly spaced hairs on inner surface and distomedial tuft of about 6 hairs. Acropodite proportionally long and narrowly terminal, about 1/3 of telopodite length, arising from outer prefemoral margin, discontinuous with and sharply demarcated from prefemur, curving broadly dorsad, sides tapering smoothly and continuously, expanding slightly apically, tip rounded.

Male paratypes. — The only variation of the male paratypes is that the telopodites *in situ* sometimes extend well beyond the caudal aperture margin, terminating over the sternum between the 9th legs. The structure and configuration of the aperture and gonopods are as described for the holotype.

Female paratype. — Length 15.8 mm, maximum width 2.6 mm, W/L ratio 16.5%. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal setae 1-1, frontal 2-2, genal 2-2, clypeal and labral series merging and continuing for short distances along genal borders, about 4 setae per side. Mandibular stipes without projection, corner not produced. Sterna flat, glabrous. Prefemora without lobes.

Cyphopodal aperture relatively broad, ovoid, sides elevated above metazonal surface, caudal margin elevated laterally, more so in midline, flared caudad. Cyphopods *in situ* with valves oriented transversely in aperture, tips visible. Valves (Figs. 208-209) moderately large, subequal, corners slightly extended, with lobe on ventral surface. Receptacle small, located laterad to valves at bases, partly submerged in latter. Operculum proportionally large, clearly visible on medial side of valves.

Ecology. — Unknown.

Distribution. — Known only from the type locality (Figs. 176, 212).

Remarks. — The narrowly terminal, discontinuous acropodite, sharply demarcated from the prefemur, resembles the condition in *simplex,* except that it arises from the outer prefemoral margin rather than the inner. Accordingly, the distal prefemoral shoulder is on the inner surface instead of the outer. Thus, there is no question that the narrowly terminal condition in *clavatus* is convergent with that in *simplex.*

Ecology

With so little field experience with eurymerodesmids, I cannot generalize about habitat preferences and can only report in the individual accounts my observations of the few species I have collected. However, information on vial labels and in the literature suggest that eurymerodesmids may seek shelter under almost any object in a wide array of biotopes ranging from sandy, predominantly pine Atlantic coastal habitats, to deciduous forests in the southeast and the Ouachita, Ozark, and Central Lowland Provinces, to grasslands of the Great Plains, and to xeric desertine environments of the Edwards Plateau. They often seek shelter in caves.

I was struck by the difficulty I had in finding them and by how spotty their occurrences can be. With all the winter trips that I have made to Florida, I have only encountered *v. varius* four times, and the only place that I have found it farther north is the North Carolina site. The availabie records suggest that it is common in the southeast, yet I have collected extensively in Alabama, Georgia, and the Carolinas at the proper time of year without even one accidental discovery. Conversely, local populations can be very large; for example, populations of *v. varius* can be in the hundreds if not thousands of individuals. The populations I discovered in Alachua and Duval counties, Florida, and Robeson County, North Carolina, were easily this large, and I could have taken far more specimens. Sizeable pitfall samples were also obtained from Leon and Jefferson counties, Florida, and there is a very large sample of *v. christianus* from Washington Parish, Louisiana. These aggregates suggest that *varius* would be a suitable subject for population studies.

Likewise in south Texas, *melacis* can be locally abundant. I could have taken many more individuals at the Welder Wildlife Refuge, San Patricio County, and two samples from Hidalgo and Kerr counties are quite large. The patchy distribution was evident at the Refuge, where I found *melacis* in several small thickets around the office buildings but not in similar thickets on the range. Nor did I encounter additional specimens anywhere in south Texas despite searching out similar environments and working in general areas where I knew it occurs. North of Texas and Louisiana I have only collected one eurymerodesmid, *oliphantus* from Jackson County, Illinois, despite considerable work in forests in the Ozarks and Mississippi Valley, where they are abundant judging from the extensive collections at the FSCA. In summary, I have had little success in finding eurymerodesmids anywhere, so if there is a secret to collecting them, as there is with American platyrhacids and cove-dwelling Appalachian species of *Sigmoria* (Shelley 1981, 1982; Shelley and Whitehead 1986), I have not deduced it.

According to Wood (1867), the type specimens of *impurus* were discovered under old cow dung, and Causey (1952a) remarked that two or three milliped species may be found under a single piece of dung since there is little other cover. This statement seems plausible, but I did not find a single eurymerodesmid under dung during two weeks in Texas in February 1986. I turned scores of piles in all stages of decay and dessication, but *Desmonus* (Sphaeriodesmidae) was the only polydesmoid that I encountered. The

Fig. 210. Seasonality of *Eurymerodesmus;* the number of samples with adults per month.

few eurymerodesmids that I discovered in Texas were all under fallen logs and branches.

Throughout their distribution, eurymerodesmids demonstrate marked seasonality, showing a distinct preference for the cooler months of spring, autumn, and winter. Thus, they probably will not be encountered in the summer, which explains why I only found exoskeletal fragments of one male in Texas and the Ozarks in July 1980. To illustrate this phenomenon, I combined the species and plotted the samples from each month with at least one adult (Fig. 210). Although this probably reflects field activity to some degree, I think it portrays their availability reasonably accurately. Many other millipeds have been collected in the eurymerodesmid range in the summer, so many more samples would be expected from May-September if the millipeds were present. December was the most productive month for eurymerodesmids, followed by April, February and March, November, and October. Eleven fewer samples were taken in January than in October, but 24 more than in May. Thus, the seven coolest months of the year provided 90.9% of the preserved eurymerodesmid samples with adults. Future field investigations should therefore be concentrated in these months.

Distribution

Family and genus. — Except for the Ozark and Ouachita Provinces in Arkansas and Missouri, the Eurymerodesmidae is a lowland milliped family occurring in the Coastal Plain, Central Lowlands, and Great Plains Physiographic Provinces (Fig. 1), the regions of the central, south-central, and southeastern United States with the least topographical variation. The center of diversity lies in the Coastal Plain of southern Arkansas and northern Louisiana, extending northward into the southern fringe of the Ouachita Province. Fourteen of the 25 species, 56.0% of the total known fauna, are represented there as are three of the four lineages and six of the seven species groups, the *melacis* lineage and group of Texas and southwestern Oklahoma being the sole exceptions (Figs. 211, 213, 214). The range spans such major rivers as the Pee Dee, Santee, Savannah, Chattahoochee, Alabama, Pearl, Mississippi, Sabine, Brazos, Colorado, San Antonio, and Nueces. Inland it traverses the Red and Arkansas/Canadian Rivers, two major tributaries of the Mississippi, and the southwesternmost record, the Terrell County, Texas, locality of *melacis,* is just west of the Pecos River near its confluence with the Rio Grande. In figure 1 a smooth curve is drawn around range extremes in all directions, except for the area north of the Missouri River in northern Missouri and southern Iowa. No authentic records are known from north of this watercourse, which appears to be a boundary in this part of the range. Consequently, *Eurymerodesmus* probably does not protrude into southeastern South Dakota. The irregular northern boundary indicates three separate penetrations that extend progressively farther north: one along the Atlantic Coastal Plain into southeastern North Carolina and two in the Central Lowlands Province into central Illinois and north-

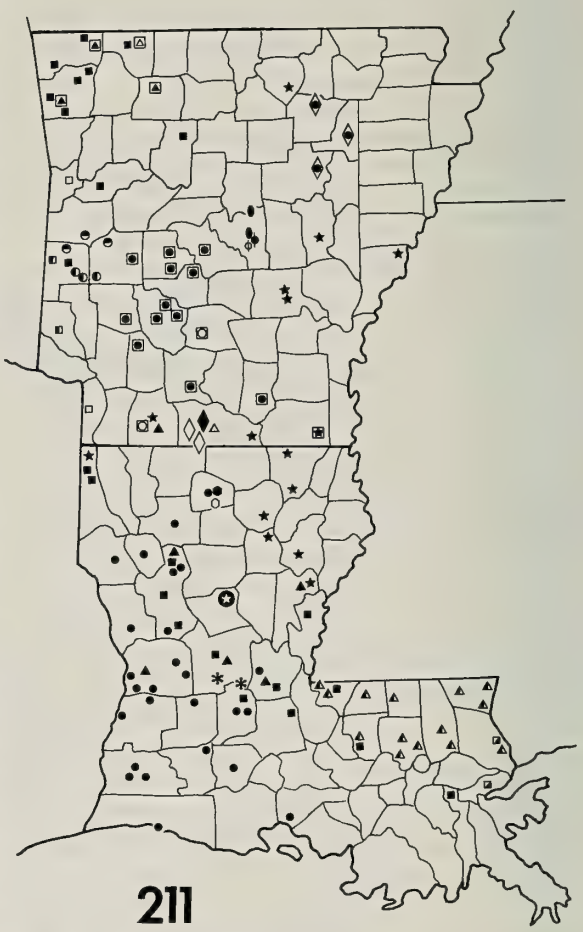


Fig. 211. Distributions of species of *Eurymerodesmus* in Arkansas and Louisiana. Star in square, *hispidipes;* stars, *angularis;* diamonds, *compressus;* vertical half-shaded dots, *goodi;* dots/circle in square, *dubius;* half-shaded triangles, *varius christianus;* triangles, *varius louisianae;* dots, *amplus;* triangles in squares, *newtonus;* dots in diamond, *oliphantus;* asterisks, *simplex;* horizontal half-shaded dots, *polkensis;* hexagons, *paroicus;* star in dot, *crassatus;* dot/circle with line, *pulaski;* ovals, *serratus;* squares, *birdi birdi;* diagonal half-shaded squares, *birdi planus;* vertical half-shaded squares, *mundus.* Open symbols denote literature records considered reliable.

eastern Nebraska. The southern boundaries are the Rio Grande, since no authentic records are known from adjoining parts of Mexico, the Gulf of Mexico, and the southern limit of the mesic deciduous woodlands in Florida, as discussed in the *v. varius* account. However, little sampling has taken place in potential sections of Coahuila, Nuevo Leon, and Tamaulipas states, so there is a reasonable probability of future Mexican discoveries.

Boundaries in other areas are less precise, but from my own field investigations, I doubt if *Eurymerodesmus* extends much farther west in Texas, or north in North Carolina. As discussed in the *melacis* account, I unsuccessfully turned countless logs and sifted through considerable litter and debris around Lubbock, Texas, and in the Davis Mountains in February 1986, so if eurymerodesmids occur in the panhandle or southwestern Texas, it is difficult to imagine where they could be other than in caves or remote, secluded ravines. Southeastern North Carolina, the area of the northernmost record along the Atlantic Coast, has been sampled extensively in all seasons of the year by biologists at the NCSM with only the one discovery of *v. varius*. I have personally searched for this species many times in the southeastern quadrant of the state, and exhaustive field work has been conducted by NCSM personnel throughout the Coastal Plain and well into southeastern Virginia. Consequently, the presently known limit, about eight miles north of the South Carolina border, is probably very close to the actual one.

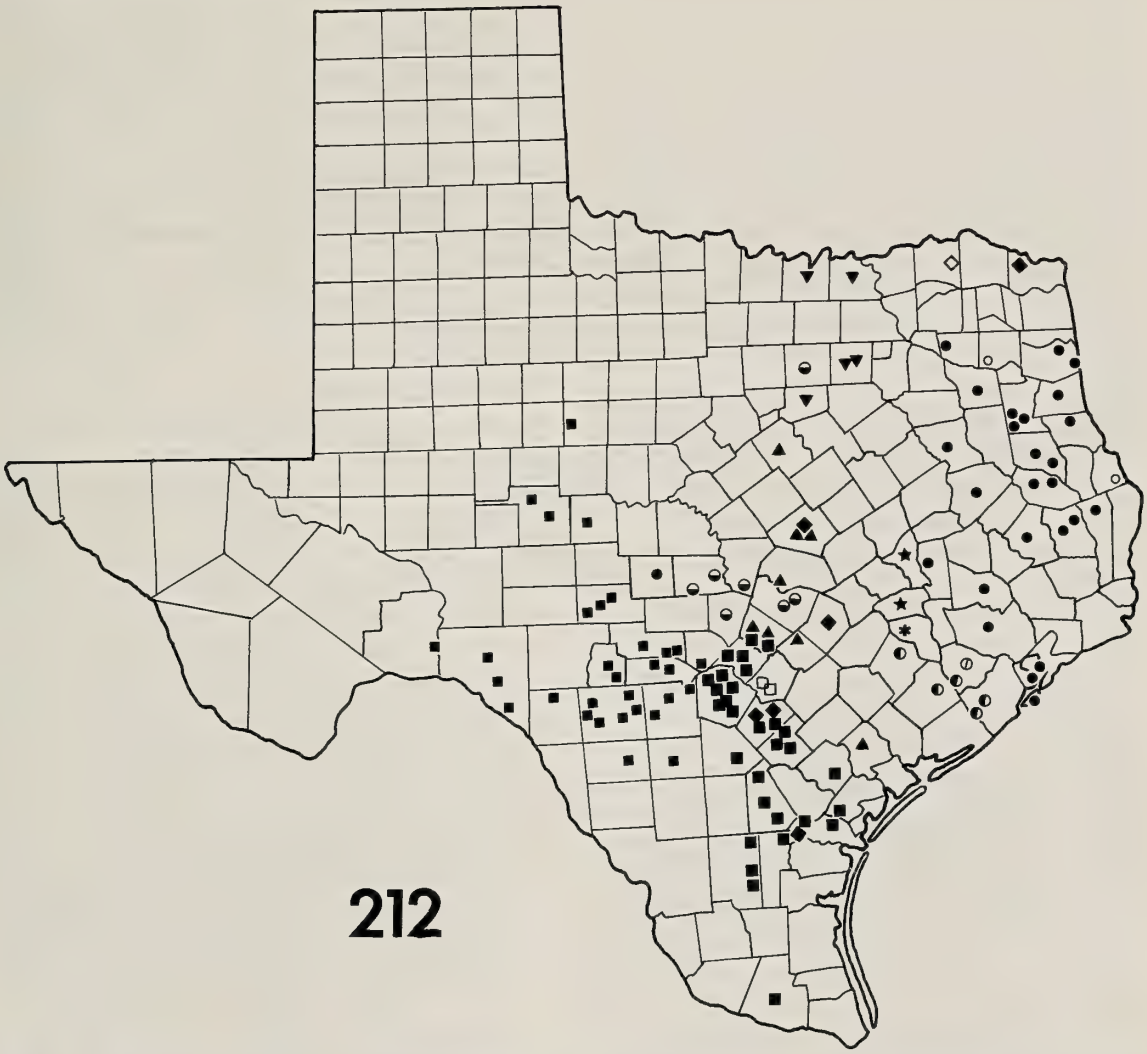


Fig. 212. Distributions of species of *Eurymerodesmus* in Texas. Stars, *impurus;* dots, *amplus;* diamonds, *birdi birdi;* inverted triangles, *mundus;* squares, *melacis;* upright triangles, *dactylocyphus;* verticle half-shaded dots, *sanbernardiensis;* horizontal half-shaded dots, *digitatus;* asterisk, *clavatus*. Open symbols denote literature records considered reliable.

Other peripheries have not been thoroughly investigated, but the western boundary in the plains states and the inland periphery in the southeast are considered reasonably accurate. The limit in Kansas approximates that of the xystodesmid *Pleuroloma flavipes* Rafinesque (Shelley 1980), which in turn correlates roughly with the western terminus of the Central Lowland Physiographic Province. The interior boundary in the southeast is generally the Fall Zone region between the Coastal Plain and Piedmont Plateau Physiographic Provinces. Such inland records as Macon, Georgia, and Auburn, Alabama, are in the Fall Zone, and there are no definite localities from the Piedmont Plateau in any state. The only regions where the boundaries are nebulous are northern Illinois, and Kentucky and Tennessee. Field work in Illinois has focused on the Shawnee National Forest in the south, but the record of *hispidipes* from Coles County, in east-central Illinois, suggests occurrence into northern Illinois, perhaps even to metropolitan Chicago if the range extends to the same latitude as *mundus* in Nebraska. Eastward expansion into western Indiana is not implausible, although the Wabash River may restrict it from the southwestern corner of this state. Thus, collecting in central Illinois and adjacent Indiana could significantly expand the family's range. No specimens have been taken from western Kentucky and Tennessee, so the line in these states is hypothetical, connecting records from Illinois and Mississippi; the family is not known to traverse the lower Ohio River as figure 1 shows. However, eurymerodesmids may be logically anticipated in the shaded areas of Kentucky and Tennessee, and perhaps as far east as the western loop of the Tennessee River.

Species, species groups, and lineages. — The *hispidipes* lineage, comprised of the single species and group, is known definitely from only two sites some 470 miles apart, one in east-central Illinois and the other in southern Arkansas (Figs. 9, 213, 214). This distance is so great as to virtually preclude extant connection. The *impurus* group (Figs. 9, 213) covers most of Arkansas except the northwest corner. It swings broadly through northern Louisiana with outlying records from eastern Mississippi, west-central Missouri, and east-central Texas. The Missouri and Mississippi forms are judged conspecific with those in Arkansas, and I connect these areas by a single line in figure 213. However, the species in Texas, *impurus* itself, has a different aperture with false pouches, and is shown as isolated (Fig. 213). The intervening area in eastern and northeastern Texas should be sampled in detail to determine if the areas connect geographically and whether anatomical connection can be demonstrated between the true pouch of *angularis* and that of *impurus*.

The *varius* group is the easternmost and most widely ranging species group, although much of the area is occupied by a single species, *varius* (Figs. 54, 213). South of the Ohio River, *varius* is the only component east of the Mississippi, and it also extends into western Louisiana and southern Arkansas. The northern part of the group's range, in Illinois, Missouri, and Arkansas, contains sizeable lacunae that need to be explored, although I show it as continuous in figure 213. Gonopodal similarities between *amplus, newtonus,* and *elevatus* suggest a continuous fauna from southern Louisiana and eastern Texas through central Missouri, and the close resemblance between all males of *oliphantus* suggests continuity between its four known areas. However, I show the westernmost record of *amplus,* from Mason County, Texas, as a small, separate area in central Texas (Fig. 213) because of the size of the intervening gap, about 190 miles, and the absence of similar forms to the north and south. The *varius* group should be expected in eastern Oklahoma, where it is currently unknown; the proximity of *newtonus* to northeastern Oklahoma suggests occurrence in Delaware, Adair, and possibly Cherokee counties.

The *simplex* group contains seven localized clusters of records, six of which comprise a reasonably compact unit in southern Arkansas, northern Louisiana, and southwestern Mississippi, although much more sampling is needed (Figs. 54, 213). The seventh area, representing an allopatric population of *serratus,* is far to the southeast in Alachua County, Florida. This site and the type locality of *caesariatus* are the only records of the *simplex* group from east of the Mississippi River, and they suggest a substantial fauna with numerous undiagnosed forms along the Gulf Coast in the Florida panhandle and southern Mississippi and Alabama.

The *dubius* group, the fourth and only monobasic group in the *Kewanius* lineage, inhabits a broad, contiguous area in southern Arkansas, where it is known from many counties (Figs. 211, 213). It may occur in northwestern Louisiana and, conceivably, even the northeast corner of Texas.

Because it is the most diverse assemblage in *Eurymerodesmus,* combining the *impurus, dubius, varius,* and *simplex* groups, the *Kewanius* lineage expectedly occupies the greatest area, around 2/3 of

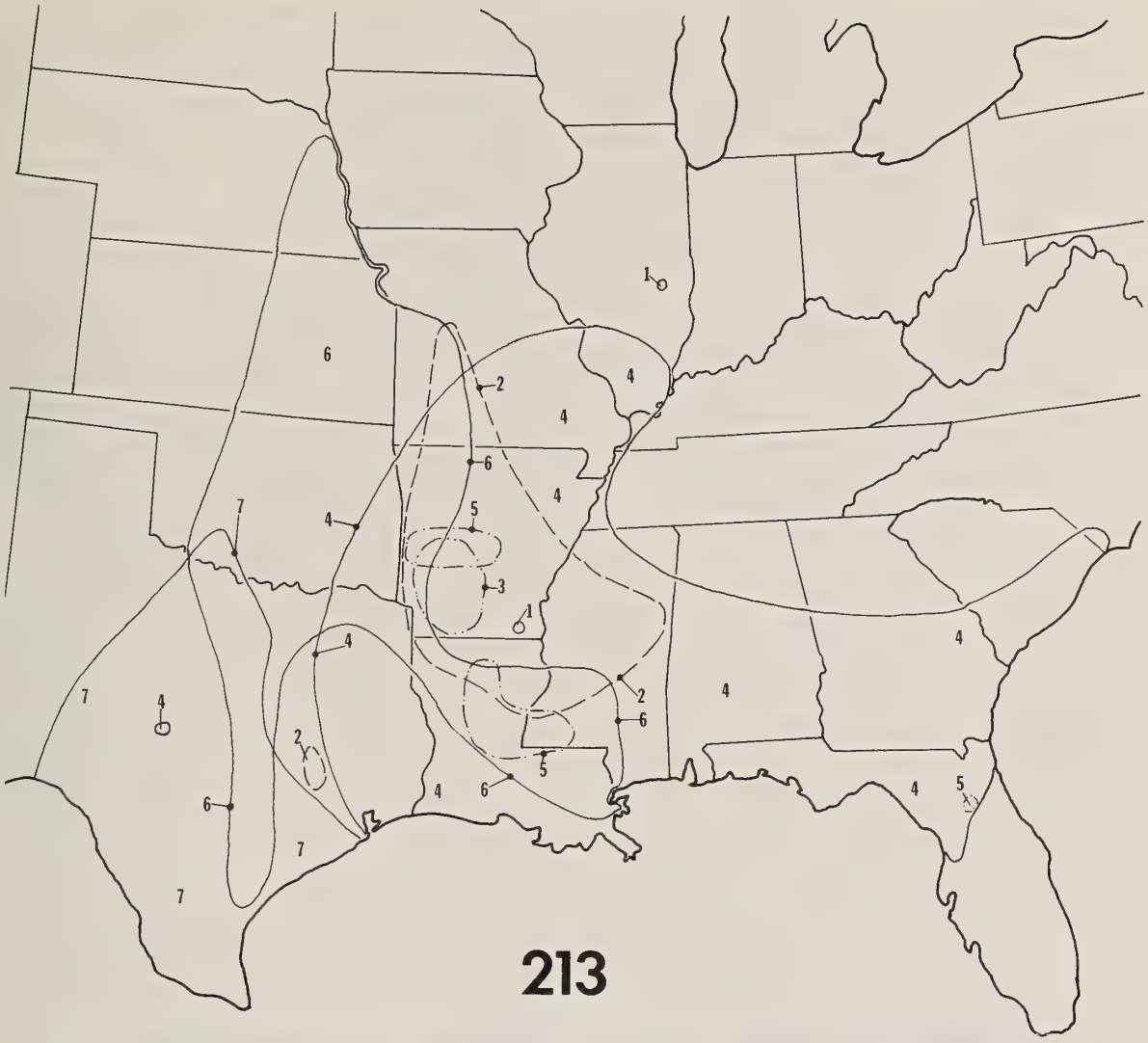


Fig. 213. Comparative distributions of the species groups of *Eurymerodesmus*. 1, *hispidipes* group; 2, *impurus* group; 3, *dubius* group; 4, *varius* group; 5, *simplex* group; 6, *birdi* group; 7, *melacis* group.

the generic range (Fig. 214). It is the easternmost lineage, covering all the area in the southeast, and it expands northward along the Mississippi Valley into Illinois and Missouri, and westward through Arkansas and Louisiana into eastern Texas and, by implication, eastern Oklahoma. It overlaps the eastern half of the *birdi* lineage and the Arkansas site of *hispidipes,* and its allopatric population in central Texas is sympatric with the *melacis* lineage. No overlap is otherwise known between the *Kewanius* and *melacis* lineages, which appear to be parapatric in southeastern Texas.

The *birdi* lineage is the northernmost ensemble, occupying the western periphery in the northern sector of the range (Figs. 147, 213, 214). It extends in a wide band from Nebraska and western Missouri into northeastern Texas, where it divides into a broad branch that penetrates across the Mississippi River into southeastern Louisiana and southwestern Mississippi, and a narrow branch that continues into south Texas. This is the most continuous assemblage in *Eurymerodesmus,* but populations of *b. birdi* in south Texas are some 214 miles from the closest records in northeastern Texas. The gap is filled by *mundus,* lending continuity to the lineage's distribution. Aside from this hiatus in *b. birdi,* there are no areas where collecting is particularly needed in the *birdi* lineage, although pinpointing the western and northern extremities would be useful.

The *melacis* lineage, the southernmost and westernmost assemblage, occupies the southwestern periphery of the genus (Figs. 176, 213, 214), over-

lapping the southern extension of the *birdi* lineage and the westernmost site of *Kewanius*. It extends from the Gulf of Mexico onto the Edwards Plateau in south-central Texas, with the inland or western border pushing northward into Oklahoma, while the coastal boundary lies south of Houston and is parapatric to the *Kewanius* lineage. Records are concentrated east of highway I-35, north of I-37, and between San Antonio and Del Rio. Little material is available from south Texas, and there is a large gap in the north-central area, where the Fort Worth record of *digitatus* is the only one between Comanche county, Oklahoma and the type locality in Burnet County, near the latitude of Austin. Because of the Fort Worth record I show a unified area for the *melacis* lineage in (Figs. 213-214), but the record in the Wichita Mountains of Oklahoma may be detached from the rest of the range. Considerable field work is therefore needed in the area bounded by the Wichita Mountains on the north, I-35 on the east, Burnet and Llano counties, Texas, in the south, and Abilene on the west.

Although the range of the Eurymerodesmidae is far from thoroughly collected and many distributional gaps remain, some lacunae between conspecific populations are so large as to virtually guarantee allopatry. For example, gaps of over 150 miles occur in *hispidipes, angularis, varius, amplus, serratus, birdi,* and *digitatus*. The largest hiatus is in *serratus,* where the Pulaski County, Arkansas, and Alachua County, Florida, populations are segregated by over 700 miles. Because of the vastness

Fig. 214. Comparative distributions of the lineages of *Eurymerodesmus*. 1, *melacis;* 2, *hispidipes;* 3, *birdi;* 4, *Kewanius*.

of the intervening region, which covers more than three states, it is hard to imagine that these populations connect today. Likewise in *hispidipes,* there is a hiatus of around 470 miles between the known populations, a sizeable gap suggesting absence of extant connection. The allopatric population of *amplus* in grasslands of the Edward's Plateau in Mason County, Texas, is isolated from the bulk of the range in forested eastern Texas by some 190 miles. In contrast to the preceding species, there are five allopatric records of *b. birdi* from four noncontiguous counties in south-central and southern Texas, the northernmost of which is about 215 miles south-southwest of the main area of the race in Oklahoma, northeast Texas, and Louisiana. These four counties are at least 70 miles apart and their localities may or may not interconnect, but together they appear detached from the rest of the range. Consequently, *b. birdi* seems to consist of two populations — a relatively continuous one extending from eastern Missouri and eastern Kansas through Oklahoma, western Arkansas, and northeastern Texas to the vicinity of New Orleans, and a smaller, subcontinuous one in southern and south-central Texas, ranging at least from Bell to San Patricio counties. The dimensions of the latter cannot be approximated from present knowledge, but it could be relatively large, encompassing much of the area from Corpus Christi and Victoria on the coast to San Antonio, Austin, and Belton inland.

The widely allopatric records of *angularis, v. varius,* and *digitatus* are more likely to be joined by future collecting, either because the lacunae are smaller, or the habitat is more uniform, or both. My reasoning is largely intuitive, but I have considerable field experience in the 275 mile gap in *v. varius* between Macon, Georgia, and Robeson County, North Carolina. I do not think that there are nearly enough differences between coastal environments in Georgia and the Carolinas for the latter populations to be isolated. This hiatus is logically a collecting artifact that will eventually be filled with material from South Carolina.

Future work. — I conclude this discussion of distribution with a review of future collecting needs. Beginning in the southeast, efforts are needed to connect the Florida and Arkansas populations of *serratus,* but it is impossible to predict where additional discoveries may be made. They are more likely in Mississippi since the eurymerodesmid fauna there is more diverse than in states to the east, where *v. varius* is the only known form aside from the one *serratus* record. Otherwise, the only future field work that is really needed east of Mississippi is material of *v. varius* from the void in South Carolina and preferably also eastern Georgia.

Meticulous field sampling, perhaps to the extent of spending two to three days in each county, is needed from central Mississippi through Louisiana and Arkansas, the region of greatest species diversity. Many more forms undoubtedly occur there, particularly in the *simplex* group. The record of *angularis* from Oktibbeha County, Mississippi, needs to be linked with the rest of the range in Arkansas and Louisiana, which should be thoroughly collected to determine the relative statuses of the various forms with long acropodites. Emphasis should be placed on Union and Columbia counties, Arkansas, to determine boundaries of *compressus,* and topotypes of *Paresmus columbus* are needed from Magnolia, in the latter county, to confirm or disprove its synonymy with *dubius.* Careful sampling is also needed in Pulaski County and environs to ascertain distributions of *pulaski* and *serratus,* which were mixed in Bollman's material (NMNH), and forms between Montgomery and Pulaski counties may tie *serratus* and *polkensis* together. Collection needs dwindle to the south and north, except for more material of *simplex* around Evangeline Parish, Louisiana, and *newtonus* in northwestern Arkansas. Specimens from central Missouri will delineate the range of *elevatus* and possibly connect it with *newtonus,* as well as close the hiatus of 216 miles in *angularis.*

In the northern part of the range east of the Mississippi River, efforts are sorely needed in central Illinois to secure more material of *hispidipes,* determine its distribution, and pinpoint the northern periphery of the family in this area. South of the Ohio River, *Eurymerodesmus* should be documented from western Kentucky and Tennessee, where new forms may be encountered.

The northern and western peripheries of the family in Nebraska and Kansas need refinement, but the only specific collecting needs are corroboration of early literature records of *b. birdi* and *mundus* as explained in their accounts. A few literature records of these species also need confirmation in Oklahoma, but the principle requirement is in the eastern, Ouachita section. *Eurymerodesmus newtonus, goodi,* and *polkensis* all occur just across the state line in Arkansas and can be anticipated in eastern Oklahoma, where only *b. birdi* and *mundus* are currently known. In southwestern Oklahoma, more material is needed of *digitatus* in and near the Wichita Mountains and southward to the Red River.

Considerable field work is needed in Texas, with emphasis on the void between Abilene and Fort Worth, and Wichita Falls and Llano/Burnet. No specimens, not even juveniles, have been taken from this substantial area where eurymerodesmids can be expected to be abundant and *digitatus, melacis,* and *mundus* may occur. East Texas has been comparatively well collected, based on the number of samples of *amplus,* but more work is needed to try to link *impurus* in Brazos County with the rest of its group in northwestern Louisiana. Marion and Harrison counties should harbor *angularis,* based on its occurrence in Caddo Parish, Louisiana, and additional representatives of the *impurus* group may exist around Nacogdoches, Huntsville, and the Big Thicket Area, where only *amplus* is currently known. South of Houston, male topotypes are still desired for *sanbernardiensis,* to eliminate doubt of its identity. In addition to more individuals of *impurus,* detailed collecting in neighboring Colorado, Waller, Austin, Washington, and Fayette counties may provide more individuals of *clavatus* and clarify the relationship between its unique gonopod and the rest of the *melacis* group. Farther south, material is needed from the slight gaps in the range of *dactylocyphus* in Gonzales and Dewitt counties, in addition to those farther north in Travis and Corzell counties. The range of *melacis* in south Texas is the best collected area of the state, but additional specimens are needed along the southern Rio Grande in the vicinities of Eagle Pass, Laredo, Hebbronville, Zapata, and Rio Grande City.

For the benefit of future workers and to complement the group and lineage range maps, I append county distribution maps for the states with the most diverse faunas, Arkansas, Louisiana, and Texas (Figs. 211-212). Except for north-central and northeastern Arkansas and the southernmost part of Louisiana, the first two states are reasonably covered with records, but larger voids exist in Texas, which, because of its greater area, could alone take several years to adequately sample. Add another two or so years for systematic field investigations in Arkansas and Louisiana, and perhaps five or more years can be spent in just these three states. When the additional time for studies in other areas is considered, it becomes obvious that research on the Eurymerodesmidae has just begun. Many questions remain to be answered, and the present system of species groups and lineages may need to be completely revamped when significantly more material is available.

Relationships

Family and genus. — The great enigma surrounding the Eurymerodesmidae is its phylogenetic affinities. There are suggestions that it is a recent derivative of the Xystodesmidae (Hoffman 1978, 1979), an appealing idea because of the close similarity in body form. Possible synapomorphies with the Xystodesmidae include the short, cylindrical, truncate gonapophyses and the gently curved to bisinuate tarsal claws, which appear to be slightly specialized because of the basal swellings. There are also similarities with the Holistophallidae, some forms of which have elaborate gonopodal apertures and strong anterior indentations. However, this family is poorly known, and the aperture traits are not manifested by all components. The constricted aperture is also associated with its modified gonopods, and thus is not homologous to that in the Eurymerodesmidae. Until family relationships are resolved, I regard the Xystodesmidae and Eurymerodesmidae as sister taxa within the Xystodesmoidea.

Apparently on an empirical basis, Hoffman (1979) arranged the Chelodesmidea as follows:

Superfamily Chelodesmoidea: Family Chelodesmidae.
Superfamily Xystodesmoidea: Families Xystodesmidae, Eurymerodesmidae, Gomphodesmidae, Campodesmidae, and Oxydesmidae.
Superfamily Sphaeriodesmoidea: Families Sphaeriodesmidae, Holistophallidae.
Superfamily Platyrhacoidea: Family Platyrhacidae.
Superfamily Rhachodesmoidea: Families Rhachodesmidae, Tridontomidae.

The Campodesmidae, Holistophallidae, and Tridontomidae were said to have around 8, 11, and 3 known species, respectively, while the Eurymerodesmidae, with 25 known species, is the smallest of the more speciose families. Most of these taxa have now been subjected to reasonably intensive studies, and the least investigated, the Sphaeriodesmidae, Holistophallidae, and Rhachodesmidae, may hold keys to subordinal affinities as may the western Nearctic xystodesmids in the tribes Harpaphini and Chonaphini, which lack the characteristic prefemoral spines found in Central American and eastern Nearctic tribes.

Species, species groups, and lineages. — Discussion of relationships within *Eurymerodesmus* is tentative because of the large number of unknown

forms that obviously await discovery. Since it will probably be decades before substantially more material is available, it is appropriate to draw conclusions from the present data. Accordingly, I present (Fig. 215) a preliminary diagram of relationships among the lineages. Unique features can be suggested only for the *melacis* branch — short telopodites, either wholly enclosed within the aperture or only slightly overlapping the caudal margin, and relatively nondescript apertures with margins usually flat or only slightly elevated — and I judge them to be plesiomorphies, although determination of polarity is hampered by incomplete knowledge of potential outgroups. Nondescript apertures are also contradicted by *dactylocyphus,* which has a broad, distinctive opening with substantial flange-like elevations at the caudolateral corners in some forms. However, neither of these traits appears in other lineages, in contrast to the characteristic lobes of the *birdi* branch, also displayed by *polkensis,* and to lesser extents *pulaski* and *serratus,* all of the *Kewanius* line. The lobes of the *birdi* lineage also are not shared by all of its components. They are absent from *birdi planus,* whose type population has a nondescript aperture like those in the *melacis* branch, a similarity reflecting convergence. Despite these difficulties, I think that *Eurymerodesmus* can be divided into these four lineages or major components, three of which, like the subgenera of *Sigmoria* (Shelley and Whitehead 1986), display geographic cohesiveness. They are undeniable geographic entities and defensible from the standpoint of geography. The exception is the *hispidipes* branch, comprised of a unique species from two allopatric populations, which does not fit in another line.

I placed *polkensis, pulaski, serratus,* and *caesariatus* in the *simplex* group, *Kewanius* lineage, because all have narrowly terminal or subterminal acropodites. However, they could equally well go in the *birdi* lineage if greater weight were placed on the aperture. The first three species possess undivided apertures with variable elevations on the caudal margins (Figs. 109, 114, 134, 137, 142, 146), whereas *simplex, paroicus,* and *crassatus* exhibit divided apertures with caudolateral pouches (Figs. 103, 123, 127). In particular, *polkensis* has strong subtriangular lobes (Figs. 109-110), very much like those in the sympatric form of *b. birdi* (Figs. 157-158). Likewise in Mississippi, the largely unadorned aperture of *caesariatus,* with only very slight, indistinct elevations at the caudolateral corners (Fig. 117), is shared with proximate forms of *birdi planus* (Figs. 162, 165). Thus, these four species combine features of the *simplex* and *birdi* groups in the gonopods and aperture, respectively, and the undivided apertures of *goodi* and *dubius,* of the *impurus* and *dubius* groups, may also reflect genetic influence of *birdi.* Thus as with the subgenera of *Sigmoria,* the *birdi* lineage is a distinct geographic entity, but it is incompletely detached from the *Kewanius* lineage. These forms in the area of overlap exhibit features of both lines, whereas other forms in this area, for example *amplus, angularis, paroicus, crassatus,* and *simplex,* do not show characteristics of *birdi.* Consequently, the *birdi* and *Kewanius* lineages demonstrate the phenomenon labeled "incomplete synapomorphy" by Shelley and Whitehead (1986).

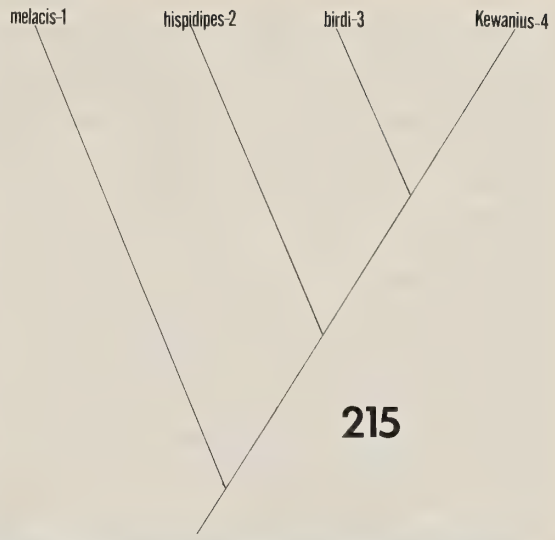


Fig. 215. Relationships of lineages in *Eurymerodesmus.* The numbers refer to figure 214.

Another problematical species is *clavatus,* placed in the *melacis* lineage because of its small size and relatively unadorned aperture (Fig. 205). Geographically, the only other possibilities are the *varius* and *impurus* groups, *Kewanius* lineage, all of whose species possess either long acropodites or divided apertures with pouches and broadly terminal acropodites, respectively. Consequently, *clavatus* would disrupt the harmonies of these ensembles, but its narrowly terminal acropodites are also divergent from other forms of the *melacis* lineage, not to mention unique to the genus, since they arise from the outer, rather than the inner, prefemoral margins. The acropodite of *clavatus,* proportionately slightly longer than those of the other species of the *melacis* branch, may reflect genetic influence of the parapatric species, *impurus,* and may be an example

of "incomplete synapomorphy" between the *melacis* and *Kewanius* lineages.

Notwithstanding these questionable species, I think that the *impurus, varius, simplex,* and *dubius* groups unite to form a coherent ensemble, which is incompletely detached from the *birdi* branch. As stated earlier, these four groups are distinguished on the basis of acropodal features for convenience and to facilitate comprehension of the genus, but they are closely related and contain all forms with divided apertures and pouches, or with gonopods or apertures similar to such forms. For example, *goodi* lacks pouches, but its gonopods possess long acropodites similar to those of *angularis,* which has pouches. Conversely, *dubius,* parapatric to *goodi,* has upright telopodites with short, broadly terminal acropodites that are only very slightly curved, but its aperture is shared with *goodi.* I assigned *goodi* to the *impurus* group because of the long acropodite, which excludes *dubius.* Nor does *dubius* fit in the *varius* group, whose components display divided apertures with pouches, and variably curved to leaning telopodites. The only alternative for *dubius* is a separate species group, which is part of the parent lineage because of the shared aperture configuration with *goodi.*

Elsewhere, the *simplex* and *varius* groups blend together through *varius* itself, since *v. christianus*, with a distally lobed prefemur and a broadly terminal but sharply discontinuous acropodite, bridges the anatomical gap between the subterminal or narrowly terminal, and therefore discontinuous, acropodites of the former, and the smoothly continuous, poorly demarcated ones of the latter. Furthermore, *angularis,* with divided apertures and pouches, connects the *impurus* with the *simplex* and *varius* groups. The pouches alone suffice for this purpose, but their variability is an important additional factor. In some forms of *angularis,* the pouches are broad and open, thereby resembling the conditions in *paroicus* and *crassatus* of the *simplex* group (compare figs. 18 and 23 with figs. 123 and 127), whereas the pouches of other forms are narrow and closed, and thus more like the conditions in *amplus* and *varius* of the *varius* group (compare fig. 21 with figs. 64 and 73). Finally, *compressus,* with a moderately long acropodite, 3/8 of the telopodite length, blends the *impurus* and *varius* groups by bridging the anatomical gap between short and long acropodites, $\leq 1/4$ and $\geq 1/2$ of the telopodite length, respectively. Thus, differences between the *impurus, dubius, varius,* and *simplex* groups enable them to be distinguished for convenience, to simplify *Eurymerodesmus,* but there are many unifying factors that merge them into a single lineage covering much of the generic range (Fig. 214, number 4). For ease of recognition this lineage is referenced by the older available genus-group name, *Kewanius,* since there is no single, representative species.

As stated previously, the *birdi* group connects with this ensemble through *polkensis, caesariatus, pulaski,* and *serratus,* and possibly also *goodi* and *dubius,* but otherwise it is detached and maintains a consistent and independent set of features in parts of Louisiana and Arkansas where they are sympatric. Consequently, I regard the *birdi* group as a separate lineage, loosely attached to, and sister to, the *Kewanius* line. With only one component species group and no available genus-group name, it is referenced as the *birdi* lineage.

The *melacis* group occupies a peripheral geographical position along the southern and western generic boundaries and is overlapped by the southern, finger-like extension of the *birdi* lineage and the allopatric populations of *amplus, varius* group, *Kewanius* lineage, to which it is otherwise parapatric (Fig. 213). There are no discernible anatomical similarities and no clear connections between the *melacis* group and the previous assemblages, the only possible exception being the slightly longer acropodite of *clavatus* that may reflect influence of *impurus.* The generally upright, sublinear telopodites of *digitatus* are phenotypically similar to, and convergent with, those of *dubius,* some 240 miles to the east. Likewise, the phenotypically similar, dactyliform cyphopodal projections of *dactylocyphus* and *compressus* are structurally different and reflect convergence. Consequently, the *melacis* group clearly represents a separate assemblage, which is referenced as the *melacis* lineage since there is no available genus-group name. Because of its generally peripheral position (Fig. 214, number 1) and the absences of both pouches and true lobes on the apertures, I consider the *melacis* lineage to be sister to the rest of the genus and family (Fig. 215). It is the least differentiated and apparently most plesiomorphic ensemble.

With only one species and two widely allopatric samples, the *hispidipes* group cannot be treated in detail. The Coles County, Illinois, site is peripheral and allopatric to the rest of the generic range, whereas the southern Arkansas locality is in the area of greatest species diversity and sympatric with both the *impurus* and *varius* groups, *Kewanius* lineage (Fig. 213). There are no unequivocal anatomical similarities with other lineages, but I detect a slight

suggestion of a distal prefemoral swelling, possibly indicating affinity with the *simplex* group, *Kewanius* lineage. Because it cannot be linked to another species, *hispidipes* comprises a separate species group and lineage whose phylogenetic position is determined by default, since the positions of the other lineages can be logically inferred (Fig. 215). However, there are also geographical and anatomical grounds for this placement, since its sympatry and the aforementioned anatomical similarity suggest closer affinity to the *birdi* and *Kewanius* lineages than is shown by the *melacis* branch. The genus-group name *Eurymerodesmus,* the oldest one in the family, is available for this line, but I hesitate to employ this name below the generic level without being certain of its usage. Future material may provide the necessary evidence to merge *hispidipes* with either the *birdi* or *Kewanius* lineages, thus clearly comprising a *Eurymerodesmus* branch. This is currently impossible, and hence, it is referenced as the *hispidipes* line.

Like *Sigmoria* in the east, *Eurymerodesmus* is a giant mosaic complex that blankets much of the southeastern and south-central United States (Figs. 1, 213-214). We are seeing this assemblage near its zenith, near maximal expansion with minimal extinction, before major anatomical and geographical discontinuities develop. It consists of four lineages or major components that overlie each other to varying degrees (Fig. 214), but since the *hispidipes* branch contains only one species, for practical purposes there are only three such ensembles. The *Kewanius* branch covers the southeastern and south-central areas and is overlapped in the western third of its range by the incompletely detached *birdi* lineage; the *melacis* line occupies the southwestern corner of the range, where it is largely independent from, and only minimally overlapped by, the other two components. Thus, the *birdi* branch is partly superimposed on both the *Kewanius* and *melacis* lineages, which are essentially parapatric (Fig. 214). Previous workers have merely extracted forms from various parts of these lineages and, because they display different combinations of the features of the apertures and gonopods, assumed that they represent distinct species and assigned new names at this taxonomic level. Not having personally collected *Eurymerodesmus* to the extent that I did *Sigmoria,* I cannot personally attest to the degree of partitioning, nor can I detail the extent to which clinal gradients traverse the range without much more material, particularly in the *Kewanius* lineage. However, the apertures and gonopods are independent of each other in the *simplex* group, reflecting influence of the incompletely detached *birdi* lineage. As the acropodite progresses from narrowly terminal to subterminal, the aperture changes from divided with pouches in *simplex,* to undivided with sizeable caudal lobes in *polkensis* and indistinct elevations in *caesariatus,* returns to divided with pouches in *paroicus* and *crassatus,* and is undivided with moderate lobes in *pulaski* and *serratus.* Trends in these two features therefore run counter to each other, but the full extent of this phenomenon is unknown.

In *Sigmoria,* Shelley and Whitehead (1986) defined species as taxa that appear segregated from geographically proximate taxa and are not connected by intergrades, hence seemingly reproductively isolated. Evidence for isolation included syntopy between phenotypically distinct forms, range disjunctions between taxa that could otherwise be considered subspecies, and abrupt range discontinuities between proximate forms, resulting in tightly fitted parapatry patterns. Subspecies were defined as reasonably homogeneous taxa that are continuous with other such taxa through intergrade or intermediate forms. I have attempted to apply these definitions to *Eurymerodesmus,* but the nature of the interfaces between forms can rarely be determined because of incomplete material. Thus, forms that appear to be parapatric and hence are considered species in this first revision may eventually need to be reevaluated. Beyond this procedural difficulty, there are interpretation problems in the *Kewanius* lineage that hinder taxonomic decisions. For example in the *impurus* group, I lumped dissimilar variants together under *angularis* but retained *compressus,* in the middle of this area, as a valid species. Though seemingly inconsistent, I think that the anatomical differences in both sexes of *compressus* (shorter acropodite, longer and dissimilar cyphopodal projections) warrant taxonomic recognition. Other interpretations of this situation are possible, and the question arises as to whether *compressus* really is reproductively isolated or a highly localized, point-form variant of *angularis.* Perhaps *compressus* actually represents a combination of stages in clinal trends in the aperture and gonopods that produce a variant of such phenotypic distinctiveness as to appear reproductively isolated when it actually is not. Similarly in the *varius* group, I combined variants of *amplus* but maintained taxonomic distinction from *varius,* although some forms of *amplus* and *v. louisianae* with intermediate densities of prefemoral hairs appear to bridge the anatomical gap between the species.

The picture is clearer in the *melacis* lineage because there is less interference from overlapping branches and because of less inherent intricacy. Relatively extensive collecting has also taken place along the interfaces between *melacis, dactylocyphus,* and *digitatus,* disclosing tightly fitted parapatric spatial relationships with minimal overlap (Fig. 176). Consequently, this situation exhibits abrupt range discontinuities, which are prevalent in *Sigmoria* and interpreted as evidence for reproductive isolation. Slight differences between *digitatus* and *sanbernardiensis,* chiefly involving the orientation of the acropodite, suggest that they may be forms of a single species, but more material is needed from intervening areas in Fayette, Bastrop, Lee, and Williamson counties. As in the *Kewanius* lineage, the question also arises as to whether the parapatric forms really are reproductively isolated and hence full species.

Thus as stated in the introduction, a question that must be posed at the conclusion of this study is whether the parapatric "species" of *Eurymerodesmus* and *Sigmoria* really are true species, reproductively isolated from each other. They facilitate comprehension of the mosaics but may be more on the order of semispecies. Perhaps the parent major components in *Sigmoria,* which demonstrate properties of species (Shelley and Whitehead 1986), and the lineages in *Eurymerodesmus* should be viewed as superspecies and hence the functional species. However, semispecies and superspecies lack nomenclatorial status and cannot be recognized taxonomically, so it is convenient to continue the practice of recognizing the localized, primarily parapatric entities at the species level, particularly since many have already been named by past authors.

The present contribution therefore applies the species category to two markedly dissimilar entities that logically should be discriminated. *Eurymerodesmus birdi* and *mundus* are broadly sympatric over a large area, unquestionably reproductively isolated, and hence unequivocal species. *Eurymerodesmus hispidipes,* with two small, widely allopatric populations, may also be such but is too poorly known to determine now. The "species" in the *Kewanius* and *melacis* lineages, however, are chiefly localized with varying degrees of differentiation. Sympatry, when it occurs, is mostly restricted to narrow zones at interfaces. Hence, the latter entities are not equivalent to *birdi* and *mundus,* so perhaps the true species in the *Kewanius* and *melacis* lineages are the lineages themselves. Consequently, a more theoretically sound view of *Eurymerodesmus* may be that it contains only five component species. This decision and the companion theoretical considerations are left to future workers.

Conclusion

Diplopodological research lags far behind that on other animals, even other arthropods, despite the impressive research potential of millipeds. Hoffman (1969, 1985) equated the state of the art with those of entomology and ornithology in the early 1800's and estimated (1985) that only about 20% of the global fauna had been described. This percentage extrapolates to around 50,000 "species" on the planet, quite possibly a conservative estimate. The prospects for the future become gloomy when it is noted that less than a dozen systematic specialists exist to investigate this large class (Hoffman 1985), with only three in the entire Western Hemisphere, all in the eastern United States. Moreover, several of the more productive and broadly-based students are at or near the ends of their careers, and few newcomers are entering the field. As currently practiced, diplopodology competes poorly with more glamorous disciplines of modern biology and may become even more neglected in the next 25-50 years, when the youngest present investigators retire. I therefore think that prudence requires a different slant to taxonomic research, that it should be directed more towards integrating knowledge throughout the class than towards the intricacies of single taxa. There are far more nomenclatorial tangles and unrevised genera than the few of us can ever clarify, and we can describe new forms indefinitely without beginning to impact on the global fauna. A major objective of scientific research is the drawing of generalities from cumulative individual observations, and if this is ever to happen with millipeds, it must be now while a number of knowledgeable investigators is still alive and productive. Consequently, it is timely to expand beyond purely descriptive and revisionistic taxonomy by evaluating the knowledge from such studies for possible insights into the Diplopoda as a whole. Common patterns, shared by many taxa, may hold broad evolutionary implications for the class, but these patterns must first be identified.

With revisions of two speciose mosaic complexes now complete, those of *Sigmoria* (Shelley 1981, Shelley and Whitehead 1986) and *Eurymerodesmus,* the questions arise as to how widespread the phenomenon is and whether it holds general principles for these poorly vagile arthropods. Shelley and

Whitehead (1986) noted that problem groups, in which species and genera are difficult to delineate, exist throughout the class and suggested the following as examples of potential mosaics: *Rhysodesmus, Nannaria,* and the California representatives of the tribe Xystocheirini *(Xystocheir, Paimokia, Amplocheir,* and *Motyxia)* (Polydesmida: Xystodesmidae); *Amplinus* and *Pycnotropis* (Polydesmida: Platyrhacidae); *Chondrodesmus* (Polydesmida: Chelodesmidae); and the family Rhinocricidae (Spirobolida). I have subsequently scoured the modern literature for evidence of additional complexes and suggested (1989) unspecified genera in the following families: Glomeridesmidae (Glomeridesmida); Spirobolellidae and Pachybolidae (Spirobolida); Spirostreptidae, Cambalopsidae, and Pseudonannolenidae (Spirostreptida); Conotylidae and Cleidogonidae (Chordeumatida); and Paradoxosomatidae, Chelodesmidae, Platyrhacidae, Oxydesmidae, Xystodesmidae, Sphaeriodesmidae, Polydesmidae, Fuhrmannodesmidae, Pyrgodesmidae, and Dalodesmidae (Polydesmida). I now augment this roster by listing (Table 8) all milliped genera with 10 or more known or suspected species according to Hoffman (1979); those with 20 or more congeners are denoted by asterisks. Most of these taxa have not received comprehensive or even cursory modern study and cannot be reviewed. However, the literature of many that have been investigated contains evidence of similarities to *Sigmoria* and *Eurymerodesmus,* suggesting comparable underlying phenomena. Consequently, these and unstudied genera in table 8 may be additional, but currently undetected, mosaics.

Table 8. Speciose Milliped Genera (10 or more species) (Hoffman 1979)
*taxa with ≥ 20 species

PENICILLATA
POLYXENIDA
Polyxenidae
Polyxenus - about 10 species
Lophoproctidae
Lophoturus - about 15
PENTAZONIA
GLOMERIDESMIDA
Glomeridesmidae
**Glomeridesmus* - 23
SPHAEROTHERIIDA
Sphaerotheriidae
**Sphaerotherium* - about 50
Cyliosoma - about 10
Sphaeropoeidae
Sphaeropoeus - about 12
**Castanotherium* - about 20
GLOMERIDA
Glomeridae
**Glomeris* - about 80
Trachysphaeridae
**Trachysphaera* - about 30
HELMINTHOMORPHA
POLYZONIIDA
Polyzoniida
Polyzonium - about 11
STEMMIULIDA
Stemmiulidae
**Diopsiulus* - 37
**Prostemmiulus* - about 42
**Stemmiulus* - 20
SPIROBOLIDA
Messicobolidae
Messicobolus - 14
Atopetholidae
Arinolus - 11
Spirobolellidae
**Spirobolellus* - about 80
Rhinocricidae
**Eurhinocricus* - numerous
**Salpidobolus* - numerous
Pachybolidae
Aulacobolus - about 12
**Centrobolus* - about 44
Eucarlia - about 10
SPIROSTREPTIDA
Cambalidae
**Nannolene* - about 22
Cambalopsidae
**Trachyjulus* - about 23
Hypocambala - about 10
Iulomorphidae
Iulomorphia - about 14
Pseudonannnolenidae
**Pseudonannolene* - about 30
**Epinannolene* - about 25
Spirostreptidae
Alloporus - about 17
Archispirostreptus — about 15
Gymnostreptus - about 17
**Orthoporus* - about 40
Plusioporus - about 13
Urostreptus - 11
Triaenostreptus - 10
Harpagophoridae
Zinophora - about 16
Gonoplectus - 19
Thyropygus - about 18
Remulopygus - about 10
Spissustreptus - 10
Odontopygidae
**Peridontopyge* - about 30
Chaleponcus - 19
Helicochetus - 13
Kompsoprium - 12
Patinatius - 13
**Prionopetalum* - 21
Rhamphidaropoides - 15
**Spinotarsus* - about 96
Syndesmogenus - 13
Tibiomus - 10
JULIDA
Julidae
Julus - 13
Ophyiulus - 18
**Leptoiulus* - numerous
Xestoiulus - about 16
**Allajulus* - numerous
Typloiulus - 17
**Amblyiulus* - numerous
Dolichoiulus - 19
Mesoiulus - about 10
Pachyiulus - about 15
**Anaulaciulus* - about 30
**Megaphyllum* - numerous
**Ommatoiulus* - numerous
Parajulidae
Aniulus - about 17
Bollmaniulus - about 12
Oriulus - about 10
Parajulus - about 15
Mongoliulidae
Skleroprotopus - 14
Paeromopodidae
Californiulus - 10
Blaniulidae
Blaniulus - about 10
Nopoiulus - 10
SIPHONOPHORIDA
Siphonophoridae
**Siphonophora* - uncertain
PLATYDESMIDA
Platydesmidae
**Platydesmus* - 27

To document the evidence for mosaics for specific genera in table 8 would be prohibitively long (general clues to mosaics are detailed briefly in the appendix), but the undeniable literature pattern must be acknowledged. To varying degrees throughout the Diplopoda there are statements and characterizations in publications on speciose genera resembling ones made years ago about *Sigmoria* and *Eurymerodesmus,* suggesting that these genera are other mosaic assemblages. The cumulative weight of this evidence implies that mosaic complexes are a major evolutionary phenomenon warranting serious consideration by diplopodologists. I focus here on large, speciose mosaics because their literature clues are easier to detect, but smaller, less diverse taxa can also constitute mosaics, for example the xystodesmid genus *Dicellarius,* with five species and five subspecies (Shelley 1984c). Since they are less intricate and their literature is comparatively straightforward, small mosaics are easier to grasp. They do not generate the massive confusion of large mosaics covering sizeable parts of one or more continents, so for the purposes of this contribution, table 8 is restricted to genera with 10 or more species according to Hoffman (1979). There are undoubtedly other speciose genera currently with less than 10 known species, for example *Striaria* (Chordeumatida: Striariidae), widespread in eastern and western North America. My purpose here is not to state absolutes but to alert diplopodologists to a widespread phenomenon and to encourage searching beyond parochial taxonomic and faunal interests for general underlying principles while there are still enough broadly-based workers to do so. We will never know the full intricacies of such widely-ranging genera as *Barydesmus, Chondrodesmus, Mestosoma, Orthoporus, Eurhinocricus,* and *Spirobolellus;* the necessary levels of field sampling are not currently possible, and many forms are probably becoming extinct through deforestation and habitat loss. However, diplopodologists can still attempt to infer common properties and

Table 8. (Continued)

CALLIPODIDA
- Schizopetalidae
  - *Acanthopetalum* - 15
  - *Eurygyrus* - about 14
  - *Apfelbeckia* - about 10

CHORDEUMATIDA
- Conotylidae
  - *Conotyla* - 13
  - *Taiyutyla* - 14
- Mastigophorophyllidae
  - *Mastigophorophyllon* - about 13
- Haaseidae
  - *Haasea* - about 14
- Cleidogonidae
  - **Pseudotremia* - about 25
  - **Cleidogona* - about 74
- Trichopetalidae
  - *Trichopetalum* - about 10
- Craspedosomatidae
  - *Craspedosoma* - about 10
  - **Pyrgocyphosoma* - about 28
  - **Ochogona* - uncertain
- Chordeumatidae
  - *Chordeuma* - about 12
- Anthroleucosomatidae
  - *Anamastigona* - about 12
  - *Brachychaeteuma* - 10
- Caseyidae
  - **Caseya* - 21
  - *Opiona* - 13

POLYDESMIDA
- Paradoxosomatidae
  - *Aulacoporus* - 10
  - *Aschistodesmus* - 15
  - *Eviulisoma* - 15
  - **Scolodesmus* - 20
  - *Eustrongylosma* - 15
  - *Antheromorpha* - 12
  - *Orthomorpha* - 17
  - *Tectoporus* - 14
  - *Xanthodesmus* - 14
  - *Stosatea* - about 14
  - *Catharosoma* - 13
  - **Mestosoma* - about 50
- Chelodesmidae
  - *Eurydesmus* - about 17
  - **Leptodesmus* - 21
  - *Biporodesmus* - 10
  - **Trichomorpha* - about 35
  - **Chondrodesmus* - about 40
  - *Brasilodesmus* - 11
  - *Caraibodesmus* - 10
  - *Strongylomorpha* - about 10
  - *Paracordyloporus* - about 15
  - **Amphelictogon* - 22
  - *Sandalodesmus* - 13
- Xystodesmidae
  - **Xystocheir (Paimokia, Amplocheir, Motyxia)* - uncertain
  - **Riukiaria* - about 20
  - **Rhysodesmus* - about 70
  - *Stenodesmus* - 10
  - **Brachoria* - about 28
  - **Sigmoria* - 65
  - **Nannaria* - about 28
  - *Parafontaria* - about 16
- Eurymerodesmidae
  - **Eurymerodesmus* - 25
- Gomphodesmidae
  - **Ulodesmus* - about 20
- Oxydesmidae
  - **Coromus* - numerous
  - *Lyodesmus* - about 13
- Sphaeriodesmidae
  - **Sphaeriodesmus* - 21
- Platyrhacidae
  - **Platyrhacus* - numerous
  - **Barydesmus* - numerous
  - **Psammodesmus* - numerous
  - **Aphelidesmus* - about 28
  - **Amplinus* - about 28
  - *Pycnotropis* - about 15
- Rhacodesmidae
  - *Aceratophallus* - 12
- Polydesmidae
  - **Epanerchodus* - numerous
  - **Polydesmus* - numerous
  - *Pseudopolydesmus* - about 13
  - *Scytonotus* - about 11
- Cryptodesmidae
  - *Apomus* - 12
  - *Peridontodesmus* - about 11
  - **Aporodesmus* - about 25
- Nearctodesmidae
  - *Nearctodesmus* - about 13
- Pyrgodesmidae
  - *Calymmodesmus* - about 16
  - *Docodesmus* - about 14
- Cyrtodesmidae
  - **Cyrtodesmus* - about 25
- Dalodesmidae
  - *Anaulacodesmus* - 16
  - **Icosidesmus* - about 38
  - *Dityloura* - 12
  - **Vanhoeffenia* - about 70

mechanisms, and search with open minds for basic truths applicable to the broad spectrum of the class.

Interpretation of mosaic complexes is beyond the scope of this work, but the phenomenon raises many intriguing questions. Why do so many millipeds form these assemblages, and how does this process occur? Is the phenomenon applicable to any genus? When we name and describe "species" in mosaics, are we really characterizing species or lesser entities, perhaps semispecies? As may be the case with the *Kewanius* and *melacis* lineages of *Eurymerodesmus,* do some of our proposed species groups and possibly even genera instead constitute species, thus implying that higher hierarchical levels may need to be lowered? Do mosaic complexes hold clues or explanations for other phenomena? Since partitioning coupled with extinctions isolated the highly atypical forms in the southern periphery of *Sigmoria,* could this general process explain the origins of such enigmatic geographical oddities as *Choctella* (Spirostreptida: Pseudonannolenidae) (Shelley 1989)? Could it be the former northern component of an ancient pseudonannolenid mosaic that is so anatomically dissimilar as to have appeared to require a monotypic family (Chamberlin and Hoffman 1950; Hoffman 1969, 1979) and is now so isolated as to be the only remaining Nearctic representative? Does much of today's global diplopod picture reflect stages in the formation and breakdown of mosaics, with some genera in expansion phases, others, like *Sigmoria* and *Eurymerodesmus,* near their zeniths, and still others in periods of decline, with significant anatomical and geographical discontinuities resulting from extinctions? As suggested by Shelley and Whitehead (1986) does this phenomenon in millipeds mirror ones in other poorly vagile organisms, for example certain soil insects, arachnids, and possibly even other myriapods, and could diplopods become something of a model for investigating it? Perhaps the road to significantly advancing diplopodology and attracting more students is not through classical revisions and faunistic treatments, though these are necessary, but through the entirely different route of investigations on shared *phenomena*, common to many taxa. Perhaps the few current diplopodologists, in an effort to salvage the field and heighten its appeal to outside specialists and potential new students, should concentrate more on dynamic processes and less on static descriptions, in essence focusing on what millipeds *do* instead of what they are. The dynamics of mosaic complexes seems a promising arena for future investigations that may significantly enhance our understanding of milliped evolution. With a diminishing number of specialists and a correspondingly bleak outlook, the time to pursue it is now.

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Appendix

Literature Clues to Speciose Mosaic Complexes in the Diplopoda

1. Restricted component distributions.

2. Parapatry of relatively localized components as revealed by distribution maps like that of *Eurymerodesmus* species in Texas (Fig. 212).

3. Statements about small or minor differences between species.

4. Uncertainty, confusion, and/or contradictions and disagreements among authors, particularly concerning the composition, generic positions, or taxonomic statuses of species groups.

Variations of general anatomical (usually gonopodal) patterns, like those shown by the subgenera of *Sigmoria* and the lineages of *Eurymerodesmus,* are subject to different interpretations by different authors, or the same author at different stages, which in turn lead to conflicting published opinions about generic validities, synonymies, and group compositions. When several such opinions are published, as with genera in the tribe Amplinini (Polydesmida: Platyrhacidae), a highly confused literature results, with contradictions and disagreements similar to those in *Eurymerodesmus* and *Sigmoria* before they were revised. Thus, muddled literature, a reflection of inherent intricacy, is a particularly telling clue to a potential mosaic.

A common thread in the literature of speciose genera are statements about small or minor differences between species, for example as between *melacis/sanbernardiensis/digitatus* and *elevatus/newtonus/amplus/varius* in *Eurymerodesmus* and between congeners in all subgenera of *Sigmoria* (Shelley 1981, Shelley and Whitehead 1986). In the latter genus, contiguous populations of adjacent species are often phenotypically similar because of residual ancestral character clines traversing the boundaries. Hence it was difficult to formulate definitions of many species that excluded neighboring populations of others, and initially, virtually every sample in parts of the range appeared to represent a separate species. Likewise in *Eurymerodesmus,* species definitions are difficult in the *Kewanius* and *melacis* lineages. Consequently, statements about slight differences between species in other genera probably reflect the effects of a mosaic, which should be expected when a genus appears to contain an inordinate number of species.

Index to Taxa

Synonyms in *italics,* new species in **boldface**

amplus, Eurymerodesmus — 45
angularis, Eurymerodesmus — 31

bentonus, Eurymerodesmus — 53
birdi, Eurymerodesmus — 72, 74
birdi birdi, Eurymerodesmus — 74
birdi planus, Eurymerodesmus — 77
booneus, Eurymerodesmus — 7

caesariatus, Eurymerodesmus — 64
christianus, Eurymerodesmus — 46
clavatus, Eurymerodesmus — 94
columbus, Paresmus — 38
compressus, Eurymerodesmus — 35
crassatus, Eurymerodesmus — 66
creolus, Eurymerodesmus — 74

dactylocyphus, Eurymerodesmus — 87
digitatus, Eurymerodesmus — 91
dubius, Eurymerodesmus — 38

elevatus, Eurymerodesmus — 59
Eurymerodesmidae — 18
Eurymerodesmus — 19
evides, Auturus — 7

floridus, Leptodesmus — 78

goodi, Eurymerodesmus — 36

hamatilis, Eurymerodesmus — 49
hispidipes, Eurymerodesmus — 25, 49, 55
hispidipes, Leptodesmus — 25, 49, 68, 69, 74, 78
hispidipes, Polydesmus (Paradesmus) — 25
hispidipes, Polydesmus (Polydesmus) — 25

impurus, Eurymerodesmus — 29
impurus, Leptodesmus — 29
impurus, Paresmus — 29
impurus, Polydesmus — 29

Kewanius — 19

louisianae, Eurymerodesmus — 47

melacis, Eurymerodesmus — 82
minimus, Eurymerodesmus — 43
mundus, Eurymerodesmus — 78

newtonus, Eurymerodesmus — 53

oliphantus, Eurymerodesmus — 55

Paresmus — 19
paroicus, Eurymerodesmus — 65
paroicus, Paresmus — 65
planus, Eurymerodesmus — 77
plishneri, Eurymerodesmus — 74
polkensis, Eurymerodesmus — 62
polkensis, Paresmus — 62
pulaski, Eurymerodesmus — 68
pulaski, Paresmus — 68

sanbernardiensis, Eurymerodesmus — 90
schmidti, Eurymerodesmus — 74
serratus, Eurymerodesmus — 69
simplex, Eurymerodesmus — 60
simplex, Kewanius — 60
spectabilis, Eurymerodesmus — 47

varius, Eurymerodesmus — 41, 43
varius, Leptodesmus — 43
varius, Polydesmus — 43
varius christianus, Eurymerodesmus — 46
varius louisianae, Eurymerodesmus — 47
varius varius, Eurymerodesmus — 43

wellesleybentoni, Eurymerodesmus — 31
wellesleybentonus, Eurymerodesmus — 31

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